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1913

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A
TEXTBOOK
of
MEDICAL ENTOMOLOGY

Specimen.

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FOREWORD

CAPTAINS PATTON AND CRAGG have asked me to write a Foreword to their textbook on Medical Entomology. I have much pleasure in doing so, even though the full preface written by the authors leaves me little to say and the importance of the subject is so well known that no *obiter dicta* of mine are called for.

I have watched this book through all its stages and I know perhaps better than any one else the enormous labour that has been entailed by its preparation. It covers an immense and in many places untrodden field: it is moreover thoroughly practical and the greatest care has been taken in the description of technique.

For both these reasons it will be extremely useful to all workers in Medical Entomology, and I trust that it will meet with the success which it undoubtedly deserves.

With these few remarks I leave the book to speak for itself.

DELHI,
November 25, 1913

C. P. LUKIS,
Director-General,
Indian Medical Service.

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PREFACE

One of the worst difficulties, which the medical and veterinary officer practising in the tropics has to contend with, is that of obtaining the necessary literature, and there is perhaps no subject in which this difficulty has been more felt than in applied entomology. The many excellent textbooks on general entomology are of little service, as they do not deal with the practical applications of the subject to sanitation, or with the particular forms with which the medical officer is concerned; the special papers, with the exception of those of the last three or four years, are scattered in a hundred different journals, to few of which the worker abroad can have access. With the advent of journals specially devoted to the subject the current literature has now become available, and it is possible to keep one's knowledge up to date without an undue expenditure of time or money, but the difficulty regarding the older work, much of which is of a very high order, remains the same. Many important papers are not to be found outside the larger libraries, or can only be purchased rarely and at a high price.

It is particularly with regard to the practical points which come up in the course of experiments—such as any medical officer may be called upon to carry out before practical sanitary measures directed against the insect carriers of disease can be adopted—that the isolated worker finds himself at a loss. Detailed accounts of the methods employed in breeding and manipulating insects and ticks in the laboratory, or of the internal anatomy of disease-bearing forms, are only to be obtained, if at all, by a search through a very large mass of literature in many languages. In too many cases the writers of papers confine themselves to a discussion of results, omitting altogether or giving only a brief note on the methods by which these have been obtained, and assuming a knowledge of the internal structures of insects which the ordinary medical man cannot fairly be expected to possess. In very many instances, even among the more familiar insects, information of the particular sort which is required for the successful carrying out of experiments is not to be found in any publication. We know of no account, for instance, of a method of breeding the house fly which is suitable for use in tropical countries; the only account of the anatomy of the body louse is so rare that we have not, after two years' negotiations with book-sellers, succeeded in obtaining a copy.

Our object in writing this textbook has been to supply the needs of our fellow-workers in these respects as far as possible; to compile, in fact, a guide to the study of the relations between arthropods and disease, rather than a textbook on entomology. The general plan of the work has been suggested by the difficulties with which we ourselves have had to contend, and by the questions which have been asked us by visitors to our laboratory. In so ill-defined a subject it has often been difficult to decide what to include and what to omit; a work of this nature cannot hope to be complete, and, although the book has grown in the making to be considerably larger than what was at first projected, it has been found necessary to exclude many forms of interest. At the same time it has been recognized that too close a limitation to forms of known importance would be disadvantageous. In this subject, as in any other, a certain breadth of view is essential to progress, and one has to remember that advance has depended in the past, and will assuredly depend in the future, to a large extent upon the study of non-pathogenic organisms, and the subsequent application of the results so obtained to the study of the related pathogenic forms. Very many blood-sucking arthropods which have, so far as we know at present, no connection with disease have been dealt with, and for a similar reason special prominence has been given to forms which act as the invertebrate hosts of the non-pathogenic 'natural' parasites.

In the arrangement of the matter a regular sequence has been observed as far as possible, the general features of the group, its relation to disease and its natural parasites, external anatomy, classification and description of species, bionomics and breeding habits, methods of breeding and laboratory manipulation, internal anatomy and methods of dissection, being discussed in turn, concluding with a list of papers dealing with the group. To this rule there are a few exceptions. The second chapter, dealing with the anatomy of the Diptera, is intended to serve as an introduction to insect morphology, and matters discussed at length therein are not referred to again in the anatomical portions of the subsequent chapters; the reader who has no previous experience of this kind of work is recommended, even if he proposes to experiment with insects of another order, to read this chapter first and to make himself familiar with the various organs by dissection of a few common types. As far as possible those Diptera which are of practical importance have been selected as examples for description and illustration, so that, with the aid of the index, the chapter will also serve as a guide to these forms. In the eleventh chapter practical laboratory methods, which apply equally to any order of insects and to ticks, are dealt with. It is not intended, of course, to provide a guide to laboratory technique, but merely to indicate the deviations from the ordinary methods which are necessary in dealing with insect tissues. It is not claimed that the methods advocated are the ideal ones, but they are those which have resulted from our own experience, and are, like most practical methods, the outcome of mistakes and misfortunes.

The external anatomy of the different groups, perhaps a very dry subject, has been dealt with at some length. The reason for this is that, rightly or wrongly, classification is founded almost entirely upon external features, and unless the student has some familiarity with these it is impossible for him to follow the systems of classification or to use the keys for the identification of species. In most cases the terminology used by authorities in systematic work has been retained, even if it is probably incorrect morphologically. For instance, the terminology of the thorax of the mosquito as used by Theobald is not altered either in the keys or descriptions, although, as was pointed out some years ago by Nuttall and Shipley, it is not in accordance with the anatomy of the parts; similarly, the organ of the louse, termed by Enderlein the pharynx, is referred to by that name in the keys and descriptions taken from his work, although, as pointed out in the account of the anatomy of that insect, it does not correspond to the pharynx in other orders. It is not possible to ensure finality in such matters, and the old terms are retained to avoid confusion.

In classification the system of an authority in each group has been followed; where there are several to choose from, the selection of one is to be taken as indicating merely a slight preference, and does not imply a belief on our part that the alternative systems are incorrect. For practical purposes one is often as good as another, and only future research can show which will present the most natural grouping. Such matters, we believe, can well be left to the specialist.

Free use has been made of the keys to the genera and species which have been compiled by specialists. Such keys, and particularly those which include only the species of a given locality, are of the greatest service to the isolated worker who has no type collection to refer to, and we feel that no further justification for reproducing them is necessary, than that they will become more accessible to those who have the most need of them. At present hardly a dozen of those in the text have appeared in journals which circulate in the tropics, and many have not appeared at all in the English language.

In accordance with the main object of the book, particular attention has been paid to the description of methods of breeding and laboratory manipulation. The methods which are given are, in the great majority of cases, those which we have used ourselves at the King Institute. It is not claimed that they are the only methods, or indeed the ideal ones, but they have all stood the test of experience, and have been successful in our hands. Where the methods of other workers are described they have been repeated by us in every case in which it could be done. We are only too well aware what an enormous amount of time may be wasted in finding out simple points of technique.

The sections on internal anatomy also contain a large amount of original matter. With few exceptions the descriptions have been written and the figures drawn from dissections and sections prepared for the purpose.

In the list of publications at the end of each chapter, those which include full references to previous work, and those which describe experimental methods, have been specially included. In addition, papers quoted in the text, and those to which we are specially indebted for information, are quoted. It is hoped that the short lists given will suffice to guide the reader to the literature on the subject when a library is available.

Of the incompleteness and the many imperfections of our work we are well aware, now that it is concluded. We feel, however, that we may justly ask some indulgence if we have omitted points of importance, or if the work of others has not always received the consideration which was due, for the book has been written and printed entirely in India, without access to literature other than that in our own possession and in the library of the Institute. We have also been without that friendly advice and criticism from fellow-workers which is of so much service in eliminating errors. On the other hand, a rich collection of material has always been available in the neighbourhood of our laboratory, and if we have failed to make the most of it the blame must be ours.

It is our pleasant duty to offer thanks to those whose aid has made our task possible. To Sir Harcourt Butler, head of the Education

Department of the Government of India, and to Sir Pardey Lukis, Director-General of the Indian Medical Service, we are deeply indebted, as without their encouragement and assistance the book could not have been written. We have also to acknowledge the financial aid received from the Indian Research Fund, which has enabled us to offer the book at a lower price than would otherwise have been the case. The Government of Madras have also rendered us substantial assistance. To Surgeon-General Bannerman, of the Government of Madras, we are indebted for much kindly encouragement.

We have to express our thanks to the following authors for the permission, so freely accorded us to reproduce illustrations which have appeared elsewhere: Dr. Annandale (and also to the Trustees of the Indian Museum), for the illustration of the external genitalia of *Phlebotomus*; Mr. Austen (and the Trustees of the British Museum), for the drawings of *Glossina palpalis* and *G. morsitans*, *Melophagus ovinus*, and the diagrams of the chaetotaxy of *Glossina*; Dr. Gordon Hewitt, for two drawings from his monograph on *Musca domestica*; Dr. Graham Smith, for several drawings from his paper on the proboscis of the Blow Fly; Professor Miall, for four drawings from his and Professor Denny's book on the Cockroach; Professor Minchin and Dr. Roubaud for the drawing of the internal anatomy of *Glossina*; Dr. Roubaud for the drawings, taken from his thesis, of the reproductive organs of *Glossina*; Professor Neumann, for the drawings of some ticks and parts of lice; Professor Newstead and Mr. Guy Marshall, for the drawings of *Phlebotomus papatasi* and the external genitalia of *Glossina*; Professor Oswaldo Cruz and Dr. Carlos Chagas for the drawing of *Conorhinus megistus*; the Hon. N. C. Rothschild, for the drawings of the heads of *Ctenocephalus canis* and *felis* and the manubrium of the former; Dr. Jordan and Mr. Rothschild for the drawings of the external genitalia of *Xenopsylla cheopis*; and Dr. Wardell Stiles for drawings of the spiracles of some species of *Dermacentor*. We are indebted to Mr. Austen for his kind offices in procuring for us the drawings of *Anopheles costalis* and *funestus*, and to Mr. Terzi for the admirable manner in which he has executed them.

In several instances the vagaries of the post have prevented our receiving a reply to a request for permission to reproduce; all drawings, however, which are taken from other works are duly acknowledged in the description of the plate on which they occur. We would add our thanks to the publishers of the various papers in which the above drawings have appeared. From them, as from the authors, we have met with uniform courtesy. The Director-General of the Indian Medical Service, on behalf of the Government of India, has permitted us to use the figures on Plates VI, VII, IX, X and XII, which have appeared in Memoirs by the junior author, and has added further to our indebtedness by allowing us to use the blocks. Mr. Hathaway, the publisher of Williston's *North American Diptera*, has permitted us the use of the two figures illustrating chaetotaxy, and has assured us that the author would have had no objection had it been possible to communicate with him. The publishers of the *Arbeiten aus dem Kaiserlichen Gesundheitsamte* have allowed us to reproduce the figure of the proventriculus of *Culex* by Schaudinn, the authorities of the Smithsonian Institution the figure of the Muscoidean head by Townsend, and the publishers of the *American Naturalist* the figure of Comstock and Needham's 'urotype'. We are indebted to the Entomological Society of London for permission to reproduce the figure of the divisions of the Dipterous thorax by Professor Mik, which appeared in their *Transactions.*

All the line drawings of bugs, lice, ticks and acari and all the brush drawings with the exception of those on Plate XXVI and those of *Haematopota pluvialis*, *Anopheles costalis* and *Anopheles funestus*, and some of the line drawings illustrating the anatomy of ticks, are by Mrs. Patton. The extent of our indebtedness to her is difficult to express. Any value the book may have is very largely due to her skill and to the unremitting care which she lavished on the work. In several instances details of structure and marking, not previously noted, have been picked out and drawn by her. The remaining drawings are the work of the junior author.

For the preparation of many of the drawings and descriptions it has been necessary to obtain specimens of forms not present in our neighbourhood, and it gives us great pleasure to be able to return thanks to those who have so courteously complied with our requests. We are indebted to Dr. Annandale for a large collection of named Diptera; to Professor Bezzi for a large collection of Muscids, including *Haematobia* and *Haematobosca*; to Dr. Anton Breinl for a collection of Culicidae and Muscidae from Australia; to Mr. Nathan Banks and Dr. C. Wardell Stiles for several species of American ticks; to Dr. Fantham and Mr. Wigham for specimens of *Ornithodorus moubata*; to Professor Oswaldo Cruz for specimens of *Conorhinus megistus*; to Mr. Hadwen for a collection of ticks from Canada; to

Mr. Howlett for specimens of *Ceratopogon* and *Simulium*; to Major W. Glen Liston, I.M.S., for specimens of *Phthirus pubis*; to Mr. Guy Marshall, Director of the Imperial Bureau of Entomology, for a large collection of Diptera, including many specimens of *Glossina*; to Professor Neumann, to whom we are greatly indebted on several other accounts, for a remarkably fine collection of ticks; to Dr. Nicolle, for a collection of Algerian flies; to Major Perry, I.M.S., for eggs of several species of *Anopheles*, and for imagines; to Miss Porter, for specimens of *Melophagus ovinus*; to Dr. Roubaud, for many Muscids, including *Glossina* and *Auchmeromyia*; to Dr. Shenkling, for a large collection of Muscidae; to Baron Surcouf, for many species of *Musca*, including *Musca corvina*; to Dr. Stanton, for a collection of *Stomoxys* from the Federated Malay States; and to Dr. Stephens, for specimens of *Glossina* with puparia.

We are glad to have this opportunity to express our sincere thanks to those who, with unfailing courtesy, have helped us for several years in the identification of specimens. Our acknowledgements in this direction are due particularly to Professor Bezzi, Dr. Speiser, Professor Neumann, Professor Kieffer, Professor Nuttall, Professor Newstead, Dr. Annandale, Mr. Austen, Mr. Brunetti and to the Hon. N. C. Rothschild. We are well aware of the amount of time and trouble which these gentlemen must have expended on our behalf. Mr. Distant and Mr. Nathan Banks have also helped us with advice in connection with the chapters on Rhynchota and Acari respectively. Our thanks are due to Dr. Gibson for his kindness in taking the photographs and for considerable help in translations from the German. We are also greatly indebted to Mr. T. Bainbrigge Fletcher who has kept us informed of all important papers dealing with Medical Entomology; his extensive knowledge of the literature has been most valuable.

The junior author wishes to acknowledge the facilities afforded him while at home by Professor Cossar Ewart and the staff of the Zoological Department of the University of Edinburgh, and in particular to acknowledge his indebtedness to Dr. Ashworth for a training in technique which has proved of the utmost value.

Lastly, our thanks are due to our publishers, who have borne with exemplary patience our many shortcomings; and to Messrs. Wiele and Kleine of Madras for the admirable manner in which they have reproduced the plates.

MADRAS
December 1, 1913

W. S. P.
F. W. C.

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Pages 43 and 347, *for* 'Homolomyia', *read* 'Homalomyia'.
Pages 162, 166, 319 and 409, *for* 'LATRIELLE', *read* 'LATREILLE.'
Page 183, *for* 'Neveau-Lemaire', *read* 'Neveu-Lemaire'.
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Page 192, *for* '4,300 feet', *read* '1,600'; *for* 'culcinae', *read* 'culicine'.
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Page 255, *for* 'aibimanus', *read* 'albimanus'.
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Page 326, *for* 'maceallria', *read* 'macellaria'.
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Page 406, *for* 'Caetaerhina', *read* 'Crataerhina'.
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Page 407, *for* 'Ornithoctena', *read* 'Ornithoctona'; *for* 'Sternopteryx', *read* 'Stenopteryx'.
Page 468, *for* 'Thompson', *read* 'Thomson'.
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CHAPTER I

INTRODUCTION

ENTOMOLOGY as a branch of preventive medicine is a study of recent growth, dating only from the two discoveries which initiated the modern science of parasitology, viz., the demonstration by Manson of the rôle played by certain mosquitoes in the transmission of filaria, and of the mode of transmission of malaria by Ross. The latter discovery has proved of infinite value to the human race: the two, rapidly succeeding one another, placed the relations of the blood-sucking arthropods to the vertebrates on which they feed, in an entirely new light, and opened up a vista of possibilities undreamed of before. Insects which had previously been regarded as pests, detested on account of the immediate trouble and annoyance they cause, now became suspected as carriers of disease.

Under the stimulus of Laveran's discovery of the parasite of malaria, and the proof of its causal relationship to the disease, the study of blood parasites was already progressing rapidly. Once the way was pointed out, and the conception of a complex life cycle involving a change of host accepted, our knowledge increased by leaps and bounds; every parasite present in the blood of a vertebrate was suspected of passing one phase of its existence in the body of an arthropod, and with each succeeding discovery there came a demand for further knowledge concerning the life history, bionomics, and structure of the suspected carrier. Entomology has thus become a science accessory, in some of its branches, to protozoology, a knowledge of the insect and of the conditions governing its existence being an evident necessity for the proper study of the parasites which it harbours.

It was soon recognized, however, that it is not only through their capacity to act as the intermediate hosts of protozoal parasites inimical to man, that insects become of medical and economic importance. In many diseases, such as plague and cholera, while there is no suggestion that the insect is an essential factor in the continued existence of the causal organism, it is beyond doubt that it may be the means of transmission from man to man, directly or indirectly. The rôle of house flies in the propagation of cholera, typhoid, and dysentery is now well established, and practical sanitarians take it into account in devising measures for their prevention and elimination.

From the nature of the case, medical entomology is a specialized branch of the study of insects, dealing with them only in so far as they are concerned in the mode of infection in various diseases, or are in themselves noxious. An expert knowledge of individual forms is required, rather than a general knowledge of the class. Moreover, the attention of the observer has to be directed on certain well-defined lines, which in many respects deviate from those on which the study of entomology is ordinarily carried out. The important facts to be ascertained are the relation of insects to man and domestic animals, their food, method and time of feeding, and their life histories; their relation to the disease in question, such as their distribution and its coincidence or otherwise with the area over which the disease occurs, and their seasonal prevalence; their structure and physiology, with special reference to those internal organs which will constitute the environment of the parasite after it is ingested. Such matters as the relations of groups of insects to one another, their phylogeny, classification, etc., fall more properly within the domain of the systematic entomologist, who studies the class as a whole, as a branch of general zoology. At the same time some knowledge of systematic work is a practical necessity, in order to be able to identify a suspected or incriminated species, and to follow intelligently the general literature on the subject.

Although the medical and sanitary aspects of entomology are thus limited, it must be borne in mind that the study of any organism or group of organisms is materially aided by the study of allied forms, the analogy with which provides working hypotheses. Some acquaintance with the whole class, as regards their life histories, conditions of existence, structure, etc., is therefore essential, as a foundation on which to build up an expert knowledge of the groups of practical importance. Familiarity with what occurs in non-disease carrying forms has led on many occasions to the disclosure of important facts regarding true carriers. Special attention in this connection is due to those arthropods which harbour 'natural' non-pathogenic parasites, for both the parasite and its host are in many cases closely related to others which are concerned in the etiology of disease. The student will do well to remember that Ross's work on proteosoma in sparrows preceded his demonstration of the life cycle of the parasite of human malaria.

The foregoing paragraphs will explain the point of view from which this book has been written, and the arrangement of the succeeding chapters. The second chapter is devoted to the anatomy of the Diptera, the subject being dealt with at some length, in order that it may serve as an introduction to the anatomy of the other groups of arthropods. The first section, dealing with the external anatomy, includes also an account of those characters on which the accepted systems of classification are built. In the following chapters each group of arthropods which is concerned with the transmission of disease is dealt with separately, as regards classification, anatomy, and technique, etc., a list of the principal papers dealing with the group being given at the end of the chapter. For further references the lists given at the end of these papers should be consulted.

Some knowledge on the part of the reader of the diverse modes in which the arthropods may affect man and the domestic animals may be safely assumed, and it will not be necessary to enter into a general discussion of such matters here; the economic importance of the various groups will be discussed as occasion arises, so far as it falls within the scope of a book of this nature. There are, however, certain points regarding the zoological position of the blood-sucking forms which call for a brief mention.

Zoological position of the blood-sucking Arthropoda

The phylum ARTHROPODA is one of the principal divisions into which the METAZOA, or many celled animals, are divided. It is an extremely large one, and contains an enormous variety of forms. According to Shipley, at least seven-eighths of the protoplasm on the surface of the world is contained within the skins of arthropods, while in size and outward form they vary from the lobster to the most minute midge.

Briefly, the essential characters of the phylum are metameric segmentation, the presence of jointed appendages, typically one pair to each segment, and a more or less hard exo-skeleton; the heart is dorsal in position, and the nervous system ventral, except in the head, where a part of the brain is dorsal; the body cavity is a haematocoele. The phylum is divided into five classes, as follows:—

CRUSTACEA:	Crabs and lobsters, shrimps, cyclops.
PROTRACHEATA:	Peripetus.
MYRIAPODA:	Centipedes and millipedes.
INSECTA:	Insects. (Sometimes called hexapods).
ARACHNIDA:	Spiders, ticks, mites.

It is only in the last two classes that blood-sucking forms occur. The INSECTA are distinguished by the following special characters. The body is divided into three well-marked regions, the head, thorax, and abdomen. The head bears one pair of antennae, and three pairs of variously modified mouth appendages. There are three pairs of legs in the adult, and generally two pairs of wings. The abdomen bears no appendages as a rule. Metamorphosis is usually complete, the young differing markedly from the adults.

The class is divided into a number of orders, in only four of which are there blood-sucking forms. These are as follows :—

DIPTERA : Flies.	These are distinguished at once by having only one pair of wings, the metathoracic pair being represented by the halteres. The larva is a maggot-like creature, distinguished from the beetle larva by the absence of legs.
SIPHONAPTERA : Fleas.	These are wingless insects, with the body laterally compressed. Metamorphosis is complete, the early stages resembling those of the Diptera. All are blood-sucking and parasitic.
RHYNCHOTA or HEMIPTERA : Bugs.	Characterized by a jointed suctorial proboscis, which can be folded under the head. The prothorax is distinct from the other segments, and the body compressed in the dorso-ventral direction in those forms which are parasitic. Many feed on vegetable juices.
ANOPLURA : Lice.	Small wingless insects, with a soft integument. The thorax is indistinctly segmented, and the body compressed in the dorso-ventral direction. All are parasitic.

The ARACHNIDA are distinguished by having the head and thorax fused into one mass, the *cephalothorax*; the remainder of the body does not usually consist of distinct segments. There are no antennae. The first pair of appendages, corresponding to the mandibles of insects, are called the *chelicerae*, the second the ***pedipalps***; when the second pair has a jaw-like portion, the two may be fused with the second maxillae to form the labio-maxillary dart or ***hypostome***. There are four pairs of legs in the adult. The alimentary canal is straight, and the anus ventral, not terminal. Metamorphosis is incomplete, the young generally resembling their parents.

The blood-sucking forms are confined to one order, the ACARINA, in which the body is soft rather than rigid, is non-articulated, and usually either rounded or oval. The thorax and abdomen are fused together as a rule, though they may be separated by a groove, the anterior portion being spoken of as the *capitulum*. The mouth parts are adapted for the purpose of attaching the animal to its host while sucking. Respiration is carried on by tracheae, the position of the stigmata or respiratory openings being important in classification. Metamorphosis is incomplete, the larva resembling the parent, but possessing only three pairs of legs, while the nymph and adult have four. The order is divided by Ray Lankester into seven suborders, only four of which concern us.

Suborder	METASTIGMATA.	Acarina in which the integument is mostly hard; a pair of stigmata is situated above and behind the base of the fourth legs. This suborder contains the *Gamasidae*, and the *Ixodidae*. It is to these two families that the blood-sucking acari, ticks, and mites belong. (Chapters viii and ix.)
Suborder	PROSTIGMATA.	Acarina in which the stigmata when present lie close to, or above the base of the chelicerae; they are absent in some of the aquatic forms. The integument is soft, but with sclerites; those on the ventral surface apparently represent the proximal segments of the legs embedded in the body. This suborder contains the families

		Trombidiidae, *Hydrachnidae*, *Holacaridae*, and the *Bdellidae*.
Suborder.	ASTIGMATA.	Degenerate acari with soft skins and no tracheae ; they are parasitic and approach the PROSTIGMATA in the development of the integumental sclerites. This order contains the *Sarcoptidae*.
Suborder.	VERMIFORMIA.	Degenerate acari without tracheae and eyes ; the posterior portion of the body is protruded into an annulated tail ; the four pairs of legs are short, and three-jointed. This order contains the *Demodicidae*.
ARACHNIDA INSERTIS SEDIS.		PENTASTOMIDA show many distinct arthropod characters ; they will be dealt with in Chapter x, Section 1.

It will be noticed that the blood-sucking forms are distributed somewhat irregularly throughout the ARTHROPODA, and are not confined to any one order, though some orders, such as the Siphonaptera, are exclusively blood-sucking and parasitic. The habit is in itself no indication of relationship, as is shown by the fact that it may be present in the female and absent in the male. Mouth parts which have become adapted for the purpose of piercing the skin and sucking up fluid nourishment are, in fact, formed from the same elements as those which are adapted for the ingestion of solid food, or fluid obtained from other sources. The mouth appendages, that is, the mandibles and first and second maxillae, are of such a type that they can, without any very great divergence from their ancestral form, be adapted to serve such a purpose. The form of apparatus which has evolved in the different families necessarily shows a good deal of variety, but it can usually be resolved into portions corresponding with the mouth appendages of non-blood-sucking forms. In the ticks, for instance, the mandibles or chelicerae make the wound, while the sucking tube up which blood is drawn is formed by their apposition to the hypostome. In the bugs the mandibles and maxillae are of great length, the former being so apposed as to form a channel with a circular lumen, while the maxillae are armed with cutting teeth and are used to pierce the skin. In the Diptera the piercing appendages may be the mandibles and first maxillae, or the second maxillae, while the sucking tube is formed by the outgrowth from the pharynx of two spatulate slips, one dorsal and the other ventral. Secondary modifications, such as flattening of the body, leathery consistence of the skin, etc., are developments consequent on the adoption of a parasitic habit.

Geographical Distribution

For the purpose of defining the distribution of animals, the surface of the earth is divided by zoologists into certain areas. According to Wallace, Sclater, and others, there are six regions, as follows:—

Palaearctic:	Europe, the temperate parts of Asia, and the north of Africa; Iceland and the islands in the Atlantic. It is limited by the Himalayas and the Indus.
Ethiopian:	Africa, including its islands, except the north; Arabia.
Oriental, or Indian:	India and the neighbouring islands, Ceylon, Java, Borneo, etc.; it includes also the Philippines.
Australian:	The Continent of Australia, New Zealand, the Celebes, and the neighbouring islands.
Neartic:	America north of Mexico, and Greenland.
Neotropical:	Mexico, the West Indies, Central and South America.

CHAPTER II

SECTION I

ANATOMY AND PHYSIOLOGY OF THE BLOOD-SUCKING DIPTERA

THE anatomy and physiology of the blood-sucking arthropods concern the parasitologist in two ways. In the first place, some acquaintance with the external characters by means of which the various forms are separated from one another is essential, in order that the systematic position of the particular species with which one is concerned may be determined ; the published descriptions of species are written in highly technical language, and without some general knowledge of the structures to which the terms are applied it would be impossible to follow them. Secondly, a good working knowledge of the internal anatomy is indispensable in the study of the parasites of insects. Without such knowledge the relations of the parasite to its host, and its possible wanderings in the body of the host, cannot be properly understood. Moreover, unless one knows the relations of the internal structures to one another and to the exo-skeleton, one cannot arrive at a satisfactory method of performing routine dissections.

In this chapter it is proposed to deal with the Diptera from the points of view suggested above, describing the structure and indicating as far as possible the function of the parts. In doing so the general principles of the anatomy and physiology will be explained as occasion arises, in order that, these having once been dealt with, they need not be further referred to in connection with the other blood-sucking insects. The structure of these will be considered under their separate chapters, as they differ too much in their general arrangements to be conveniently considered together with the Diptera. The examples dealt with will be almost entirely blood-sucking flies, and the statements made are not necessarily generalizations for the whole order, unless this is stated or implied.

As regards textbooks on insect anatomy and physiology, Packard's will be found most useful, though it is now out of date. Berlese's large and fully illustrated work is very valuable for reference, and contains an extensive bibliography. Most of the larger works on zoology contain a certain amount of general information on the subject, dealt with mainly from the comparative point of view. To those who have no previous acquaintance with structural entomology Miall and Denny's account of the cockroach is strongly recommended; the authors have used their type to set forth in a masterly fashion the main points in the anatomy and physiology of insects, and there could be no better preparation for work with insects than the study of this admirable little book.

A list of papers dealing with particular forms is given at the end of this chapter, and the worker may consult these as occasion arises. For further references, especially to the older and less accessible literature, the bibliography in Berlese's book, or the lists given in the special papers, may be consulted. Most of the papers of practical value are comparatively recent, and are to be found in the larger libraries.

GENERAL STRUCTURE

Insects present the characteristic features of the phylum ARTHROPODA, that is to say, they have a more or less elongated body, with a mouth at one end and an anus at the other, a central nervous system concentrated in the head, and a ventral chain of ganglia; the body is metamerically segmented, and each segment bears typically a pair of jointed appendages; the body cavity is not a true cœlom, but a haematocoele, in communication with the dorsal blood vessel. The class INSECTA is specially distinguished by the separation of the body into three well-defined regions, the head, thorax, and abdomen; only three pairs of legs are present, and there are usually two pairs of wings. The order DIPTERA is separated from other insects chiefly by the transformation of the hind pair of wings into the structures known as halteres or balancers, and by the adaptation of the mouth parts to form a sucking organ.

By metameric segmentation is meant, that the body of the animal is made up of a number of separate segments or metameres, arranged one behind the other in the long axis of the body. (Plate I, fig. 3.) In insects there are said to be typically about twenty segments, of which the first six go to form the head, the next three to the thorax, and the remainder to the abdomen. Each segment should bear a pair of appendages, but in the adult insect only those on the head and thorax remain, and those on the head are always very highly modified. It is possible that certain parts of the external genital organs are the representatives of true abdominal appendages. At a very early stage in the evolution of insects each metamere is believed to have been a replica of its neighbour, and this condition of affairs is found to a certain extent in the early stages of the present forms; but in the adult the primitive arrangement of the segments is obscured, and can only be recognized in certain parts of the animal. The most obvious segmental markings are to be found in the exo-skeleton, and particularly in the abdomen, and the term 'segment' has come to be used with a special meaning in this connection. In the head there is little trace of the original arrangement to be found, and the extent of the various segments is a debatable matter. In the thorax each segment bears a pair of legs, but on account of secondary changes brought about by the growth of the wings the segments have developed unequally. In the internal anatomy the only organs which show traces of a segmental arrangement are the tracheae or breathing tubes, of which there are as a rule one pair to each segment, and the ventral chain of nerve ganglia.

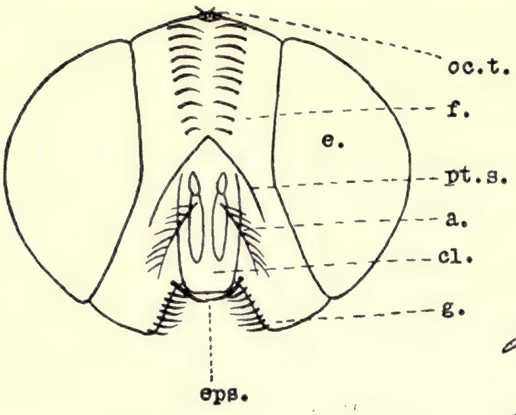
The Diptera are the most highly specialized as well as one of the most numerous orders of the class, and in them we find that the fusion of the segments has gone further than in other orders. As a result of the great development of one pair of wings, with the muscles which act upon them, the middle segment of the thorax has become greatly increased in extent at the expense of the others. In the abdomen there is, throughout the order from the simple forms upwards, a general tendency to a reduction in the number of the visible segments, and a corresponding concentration of the internal structures. This is frequently accompanied by a transformation of the exo-skeleton of the terminal segments into organs connected with the function of reproduction.

The exo-skeleton and its appendages

Insects, like other arthropods, possess a more or less rigid integument, which encloses and protects the soft parts, and at the same time provides attachments for the muscles of the body, all of which have their origins and insertions on the internal surface of the exo-skeleton. The appendages consist of outgrowths of the integument, containing muscles, nerves, and other structures, and the joints in them are formed by a moulding of the outer layer. There is no true internal skeleton, but the exo-skeleton sends inwards certain processes, often termed the endo-skeleton; these occur in situations where either greater structural stability or additional surface for muscle attachment is required.

The nature of this integument is of considerable importance from

PLATE. I.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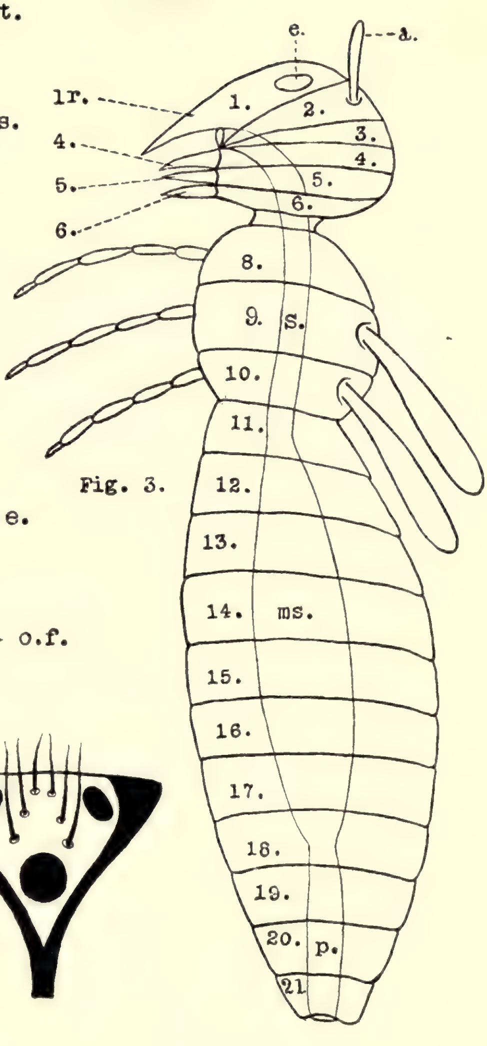
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Fig. 3.

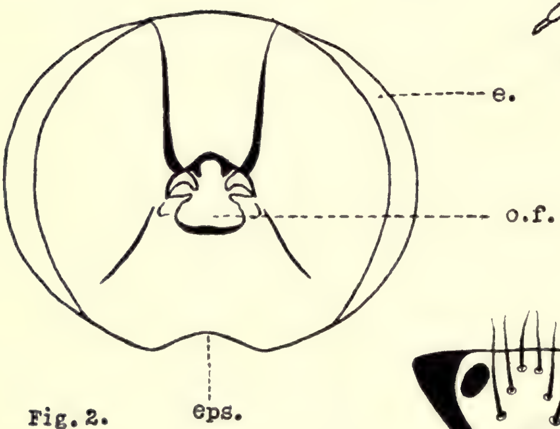

Fig. 2.

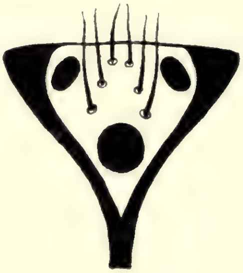

Fig. 4.

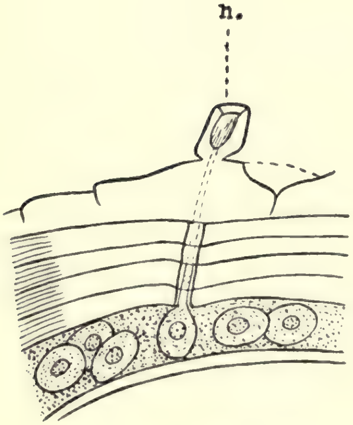

Fig. 5.

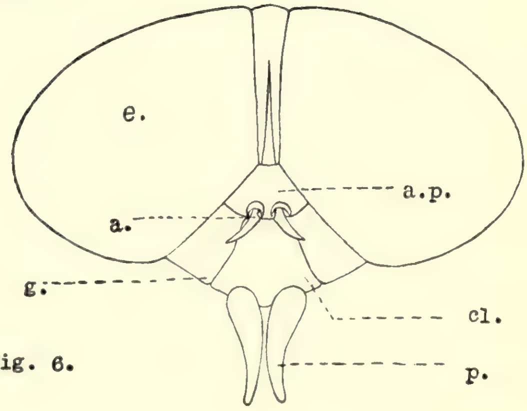

Fig. 6.

PLATE I

Figure 1. Head of a Muscid fly, seen from the front, with the proboscis removed. pt.s., the ptilinal suture. f., frons. oc.t., the ocellar tubercle (shown enlarged in figure 4).

Figure 2. The same, seen from behind.

Figure 3. Diagram showing the segmentation of a primitive insect, after Berlese. The segments are numbered in order. Six are shown in the head, five only being represented in most insects. The last three head segments have appendages, which become a part of the proboscis in the Diptera. The course of the alimentary tract is indicated. s., stomadaeum. ms., mesenteron. p., proctodaeum (page 101).

Figure 4. The ocellar triangle of *Musca*, showing the three pigmented ocelli and the ocellar bristles.

Figure 5. A section through chitin, to show the chitinogenous cells and the laminæ. h., a hair, in direct connection with a chitinogenous cell. From Miall and Denny.

Figure 6. Head of male *Tabanus* seen from the front. An example of a holoptic fly. Compare Plate III, figure 3.

REFERENCE LETTERS, PLATES I TO VII

Letters not included below will be found in the descriptions of the plates

a.	Antenna.
a. p.	Antennal plate.
b. c.	Buccal cavity.
c.	Cardo.
cl.	Clypeus.
d. b. c.	Dilator muscle of the buccal cavity.
d. d. ph.	Dorsal dilator muscle of the pharynx.
d. ph.	Dilator muscle of the pharynx.
e.	Eye.
ep.	Epipharynx.
eps.	Epistomal orifice.
f. ch.	Food channel.
g.	Gena.
gl.	Galea.
hy.	Hypopharynx.
i. t.	Intracranial tunnel.
l. ep.	Labrum-epipharynx.
lb.	Labium.
lbl.	Labellum.
lr.	Labrum.
m.	Mouth.
mb.	Membrane.
mn.	Mandible.
mt.	Mentum.
mx.	Maxilla.
oc. f.	Occipital foramen.
oes.	Œsophagus.
p.	Palp.
ph.	Pharynx.
pr.	Prestomum.
sl. d.	Salivary duct.
sl. p.	Salivary pump or valve.
sm.	Submentum.
st.	Stipes.
tr.	Trachea.

the point of view of technique. Rather less than half its total weight consists of the substance known as *chitin*, the peculiarly resistant properties of which are a formidable obstacle in the manipulation of insect tissues. Chitin is insoluble in acids and alkalis, in alcohol and ether, and in fact in all the ordinary laboratory reagents. It is also extremely impermeable, and unless apertures in the integument are made reagents will not penetrate to the soft tissues. It is pigmented, and when free from cellular material is more or less transparent. Its colour can be readily removed by bleaching agents, such as chlorine gas. At the moment of emergence from the pupal covering the chitin of the imago is soft and colourless, and it is only after exposure to air and light that it becomes pigmented and rigid. When in thin layers, with much cellular material, it forms a tough membrane, but when in thick sheets it has only a small amount of resilience. It resists the action of heat, but is made harder and more brittle by even such moderate temperatures as are used in a paraffin bath. Prolonged immersion in alcohol has the same effect.

The disposition of the chitin in the integument is as follows. (Plate I, fig. 5.) On the internal surface of the exo-skeleton there is a single layer of cells set on a thin basement membrane. These are the chitinogenous cells, and external to them there are found many layers of solid and structureless chitin, which has been secreted by the cells in very much the same manner as that in which the nails of vertebrates are produced. The basement membrane and the chitinogenous cells form a continuous layer throughout the body of the insect, and there is always a layer of chitinous tissue external to them, the thickness of which is varied in accordance with the structural requirements. In such parts as the thorax, where strength is necessary on account of the great development of the wing muscles, the layer of chitin is very thick, while in the region of joints, where flexibility is required, it is thin. But it is important to remember that even in thin sheets chitin is quite impermeable to any of the ordinary fixatives.

The hairs and scales which are present on the integument, and which are so much used in classification, are outgrowths from the exo-skeleton. They are of two kinds, sensory hairs and others the function of which is unknown. The sensory hairs, such as those found at the distal end of the proboscis, on the palps, and on the antennae in some forms, are hollow, and contain delicate filaments of nervous tissue, enclosed in a central canal. They arise from single cells of the chitinogenous layer, the base of each hair piercing the chitinous laminae, and emerging from the integument at a small pit. At the base there is a small bipolar ganglion cell.

In the Muscoidean flies the integument is adorned with many large bristles, called *macrochaetae.* These are arranged in a definite manner, providing most useful characters in classification. Since their value was pointed out by Osten Sacken great attention has been paid to them by dipterologists. A discussion of chaetotaxy, as this branch of descriptive entomology is termed, will be deferred until the regions on which they occur have been described.

Osten Sacken has some interesting remarks on the possible function of these large bristles. It had been previously suggested by Macquart that their purpose was to protect the fly from collisions, such as its rapid flight might render it liable to, and the ingenious author carries this suggestion a little further. He points out that macrochaetae occur almost solely in those flies which are pedestrian in habit, using their legs in the search for food, in attacking other insects, and in oviposition, while in those flies which are mainly aerial in habit, and use their legs only for alighting, large bristles are rare. In *Tabanus*, for instance, which merely uses its legs so far as is necessary in finding a suitable place to make a wound in the skin of the host, the bristles are insignificant, while in the domestic house flies, which run about over the food surface, and search place after place, the bristles are well developed. In the Tachinidae, which parasitise caterpillars, many large macrochaetae are always present. It is evident that flies of an aerial habit, which spend their lives mainly either at rest or on the wing, and which have moreover the faculty of poising or hovering, will be much less liable to sudden collisions than those which have a pedestrian habit. He concludes that the macrochaetae are organs of orientation, fulfilling much the same function as the whiskers of a cat.

The nomenclature of the exo-skeleton

The exo-skeleton is not of uniform thickness throughout, but is divided up into numerous plates, each of which has received a distinctive name; these are often separated from one another by membraneous intervals. The divisions are mainly in the transverse direction, and represent typically the lines of separation of the metameres; in the Diptera, they are, of course, greatly modified from the primitive condition, and it is often a matter of some difficulty to decide which of the primitive plates a particular portion of the integument may represent. The subject is of academic rather than of practical importance, and it will suffice if it is touched on it only so far as to explain the terms in use.

Audoin supposed that the exo-skeleton of a primitive segment was composed of eight chitinous plates, arranged in pairs, two dorsal, two ventral, and two lateral plates on each side. Although this is not generally accepted as a type to which the very numerous and diverse forms may all be referred, his nomenclature has been preserved, with some modifications. He termed the dorsal plates the *terga*, the ventral the *sterna*, the pair of lateral plates contiguous with the terga the *epimera*, and the pair contiguous with the sterna the *episterna*. The two lateral plates when fused together are known as the *pleura*. Such a primitive arrangement is not to be looked for in the Diptera, and it is best to regard the terms as descriptive only, without laying too much stress on their significance, especially since hardly any two authorities are agreed on the point. In the head the various segments have become fused together to form a chitinous box, often termed the head capsule, and few if any really reliable indications of the original segmentation are to be found in the adult insect. In the thorax a nearer approach to the type is found, but on account of the development of extra plates, and the displacement of others, it is very difficult to refer them to the type, especially in the case of the lateral plates. In the abdomen the arrangement is simple, as the terga and the sterna are preserved, and the interval between them occupied by a soft membrane, which, as it represents the pleural plates and bears the openings of the breathing tubes, is termed the pleural membrane.

Each chitinous plate is separated from its neighbour by a narrow interval which is filled in either by soft membrane or by thinner chitin, and in this way the whole body of the insect is provided with a series of joints, which enable the various segments to move on one another. The head is united to the thorax by a flexible neck; the segments which make up the thorax are firmly welded together for the most part, but there is a membraneous interval in the lateral wall which permits of a certain amount of expansion; in the abdomen each dorsal and each ventral plate is connected with those in front of and behind it by means of a narrow strip of membrane. The dorsal plates are connected with the ventral ones by the pleural membrane.

THE HEAD—(Plates I and III)

The head capsule is a rounded and compact box, composed of the chitinous plates which belong to the exo-skeleton of the first five* segments

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* Of the six segments which should go to make up the head, the third is absent in the majority of insects.

of the body. The appendages of these segments are all highly modified for special functions, the first two in connection with the special senses, the remaining three in connection with the mouth. The head in the Diptera is relatively large, but this is not due entirely to the development of the brain, but to the presence in the head of certain large air sacs which have an important function in connection with the sucking apparatus. In addition to the brain and the air sacs, the head contains the pharynx or sucking pump, and the muscles of the head appendages. The shape varies from that of a flattened dome, as in the Tabanidae, to a more or less regular sphere, as in the Muscidae. The antero-superior surface is rounded, and bears the antennae at its most anterior point. The posterior surface is usually flattened, and may be concave. Its lower portion is occupied by the base of the proboscis, while about its middle there is the occipital foramen, to the boundaries of which the membrane of the neck is attached. The foramen is usually supported by a horseshoe-shaped arch.

The various parts of the head have received special names for descriptive purposes. Unfortunately a good deal of confusion exists in the nomenclature of this region, for many of the terms are merely distinctive names employed in systematic work, and can only be properly applied to particular groups of flies, while others have originated in attempts to determine the homology of the head.

Regions of the head

In the Orthorraphic flies the angle at which the posterior and superior surfaces join one another is termed the *occiput*. The area in front of this, which may be conspicuous, as in the Culicinae, is known as the *vertex*. In front of this, and between the eyes, is the *frons*. The eyes occupy the entire lateral regions of the head; when they are separated from one another by a definite space the fly is said to be *dichoptic*, while if there is only a very narrow interval the fly is said to be *holoptic*. The antennae arise at the anterior end of the frons, and may have at their bases a raised plate, as in the Tabanidae, in which it is known as the *callus*. Below the antennae there is a median plate, generally produced forwards, and forming the distal limit of the anterior surface; this is known as the *clypeus* or face. The region below the eyes and external to the clypeus on each side is the *gena*, or cheek. The median posterior area extending from the base of the proboscis towards the occipital foramen is termed the *gular region*. It is generally membraneous in the Orthorrapha.

In the Muscoidean flies, among which are the blood-sucking Muscidae, the shape of the head is rather rounder than in the Orthorrapha, and the structure of the wall is modified. The most striking and indeed the characteristic feature of the head in this group is the presence on the front of a long arched suture, commencing transversely above the antennae and extending downwards on each side of them, almost to the distal border. This is the *ptilinal suture*, and marks the place at which the ptilinal sac was pushed out at the time of the emergence of the imago from the puparium. The shape of the head is further modified by the increase in size of the basal joints of the antennae, which are pendulous, and rest in hollows on the anterior surface. The base of the head is also altered by the fact that a part of the wall has become merged with the proboscis, as will be explained shortly, and has become retractile. When the head is viewed from behind the whole of the posterior wall is seen to be chitinous, while at the lower border there is a rounded foramen between the anterior and posterior surfaces, through which the proboscis is protruded. The gular region has, therefore, become merged into the posterior wall of the first part of the proboscis. The aperture through which the latter is pushed out is sometimes referred to as the buccal orifice, a most unfortunate term, for it is some distance posterior to the structure universally known as the pharynx, and has nothing whatever to do with the mouth parts. It is better to use the term *epistomal orifice*, as the thin plate of chitin in front of it is known as the *epistoma*.

The terms used in describing the Muscid head (Plate III, fig. 1) are somewhat perplexing, mainly on account of their multiplicity. The area enclosed by the lateral arms of the ptilinal suture is known as the *ptilinal area*, the *facial depression*, or the *front*. It is almost entirely made up by the clypeus, for which alternative names are the *face*, *facial plate*, *mesofacial plate*. The antennae may lie in deep or shallow grooves, termed the *fossae* of the facial plate, or the *antennal grooves*. The grooves may be separated by a ridge, termed the *facial carina*, and this may be produced forwards in its lower portion. The lateral margins of the ptilinal area may be thickened into ridges, termed the *facialia*, or the *facial ridges*, or *vibrissal ridges*. They terminate in prominent angles known as the *vibrissal angles*. Below the facial plate or clypeus there is a small mesial plate, forming the boundary of the epistomal orifice, and termed the *epistoma*. The orifice itself, through which the upper part of the proboscis passes out in extension, is also known as the *oral orifice* or *buccal orifice*, and an *oral cavity* is mentioned, supposed to be bounded in front by the epistoma. Below the epistoma on the anterior surface there is a transverse plate regarded by many authors as the clypeus, the upper and larger plate referred to above being considered as derived from other parts of the head. This plate corresponds to the anterior arch of the fulcrum, and will be described in more detail further on. At the upper end of the ptilinal area there may be two small plates, the lower one of which supports the antennae; the upper one is termed the *lunule.*

The area behind the ptilinal suture is divided into three lateral portions, the extent of which will be seen from the figure. The frontalia are also known as the *frontals*, or the *mesofrontals*, the parafrontals as the *geno-vertical plates*, and the parafacials as the *sides of the face*, or *the genae.* The term *cheek* is applied to that portion which has already been described as the gena.

Most of the above terms are taken from Townsend's paper on the taxonomy of the Muscoidean flies, to which the reader who wishes to study systematic dipterology will do well to refer. The difficulty in following descriptions is not so great as the multiplicity of terms in use would suggest, for most papers are illustrated with diagrams, and the meaning of the words can be ascertained by a reference to the figures.

The Eyes

The eyes in the Diptera do not differ materially from those in other insects, descriptions of which are to be found in most text-books on Zoology. The external surface is made up of a large number of facets, usually equal in size and shape, and generally hexagonal, with rounded corners. (Plate III, fig. 2.) They may be pilose, i.e., covered with short hairs, or naked, the latter being the usual condition. They are of various colours, and the colouration may be of importance in the determination of the species; this is especially the case in the Tabanidae, in which the eyes are most beautiful objects. Unfortunately the colour fades rapidly on the death of the fly, and both it and the markings should be noted in fresh specimens.

In addition to the compound eyes there may be two or three ocelli, situated on the vertex of the head, generally in a small raised triangle. (Plate I, fig. 4.) In the fresh state they are seen as small spots of pigment; in cleared preparations the pigment is readily dissolved out, and the situation of the ocelli shown by the clear spaces which remain.

The Antennae

The antennae (Plate II.) are sense organs, which probably have for their function the perception of sounds and air currents. They are well supplied with nervous tissue and air tubes, and have peculiar 'sense pits', in which the olfactory sense is believed to be located. They are, as previously stated, the appendages of the second segment of the head, and in all cases they retain the original form, that is to say, they are composed of a

PLATE. II.

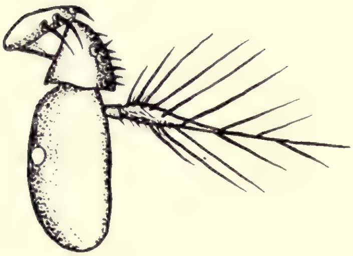


Fig. 1

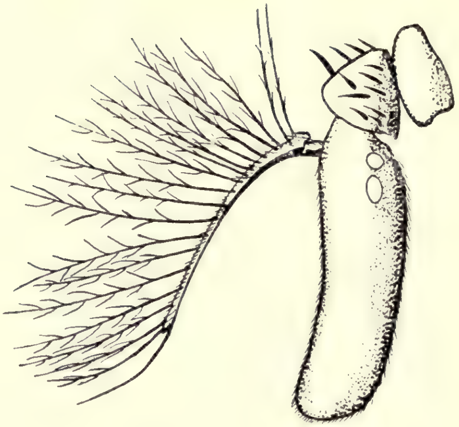
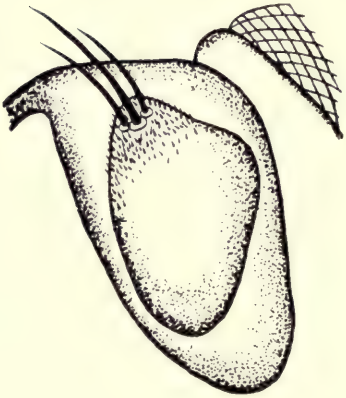


Fig. 2.



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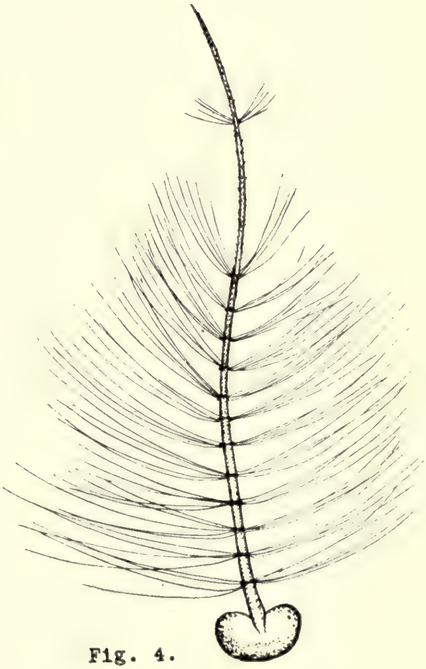
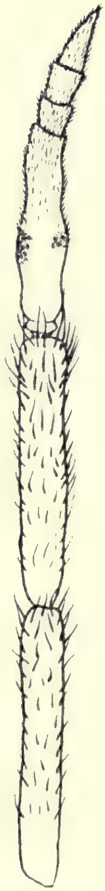


Fig. 4.



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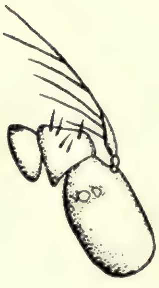

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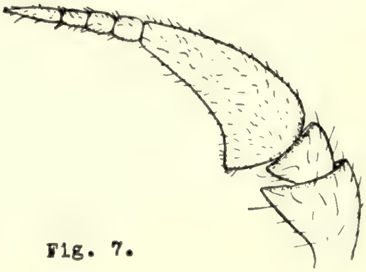

Fig. 7.

PLATE II

Types of Antennae

Figure 1. *Musca nebulo.* × 54
Figure 2. *Glossina submorsitans.* × 60
Figure 3. *Hippobosca maculata;* the short cubical antenna, consisting of only one joint, is shown in its pit. × 95
Figure 4. *Culex fatigans,* ♂ × 54
Figure 5. *Chrysops dispar.* × 36
Figure 6. *Lyperosia minuta.* × 110
Figure 7. *Tabanus albimedius.* × 42

number of joints, set one behind the other. Their appearance differs greatly in the different genera of Diptera, but in general there are two forms, one met with in the Orthorrapha and the other in the Cyclorrapha. The distinction between the two forms was used by the older systematists to divide the Diptera into the two primary divisions known as the Nematocera and the Brachycera, which correspond roughly with the two divisions named above (see Chapter III). In the Nematocera all the joints of the antenna are similar to one another, except one or two at the base, which are usually larger. There may be from four to sixteen joints, each cylindrical or sub-cylindrical in shape, and generally tapering a little from base to apex. The joints may be adorned in various ways, and the adornment may differ in the two sexes, thus offering a ready means of distinguishing them. They may be ***plumose*** in both sexes, as in *Phlebotomus*, or plumose in the male and not in the female, as in *Culex*. The whorls of hairs are attached to the base of each segment. In the Brachycerous flies the antenna consists of a small number of dissimilar joints, of which the basal ones are the most modified. In the Tabanidae, which are Brachycerous Orthorrapha, the apical joint is much stouter than the rest, and may be provided with a hook-like projection ; the distal part may be 'ringed,' or incompletely divided into a number of segments. In the Cyclorrapha, which includes all the blood-sucking Muscidae, such as *Philaematomyia* and *Glossina*, the form of the antenna is highly modified from the original shape ; it is composed of two distinct portions, the *scape* and the *arista*. The scape represents three basal joints. The first two of these are small and inconspicuous, but the third is very much enlarged and forms a conspicuous oval mass, which hangs down on the front of the head. It may be adorned in various ways, with short downy hairs or with short stout bristles, and it always shows on its anterior surface several 'sense pits', which, when seen in section, are found to be areas where the chitin is thin, and where there is a large accumulation of nervous tissue. In cleared preparations they appear as small circular clear spaces. The arista is derived from the terminal segments of the antenna. It is generally described as consisting of a single stout forwardly directed bristle, arising from the proximal end of the terminal segment of the scape, but a closer examination shows that at the junction of the arista with the scape there is interpolated another small joint. The arista may bear different kinds of smaller hairs, arranged in various ways, and its appearance is an important factor in classification. In *Lyperosia minuta* (in which three joints can be distinguished in the arista), there are five simple hairs arising from the same side, making with the termination of the central strand six equal filaments. In *Musca nebulo* there are similar simple hairs on both sides of the arista. In *Glossina* the secondary hairs are confined to one side, and each of them bears a set of five or six pairs of smaller hairs, giving the organ a plumed appearance. The central strand of the arista is termed the ***flagellum*** by some authors.

In other families of Diptera conditions intermediate between these are found. For instance, in the Asilidae, a family of predaceous flies allied to the Culicidae and the Tabanidae, the antenna consists of three joints like those of a Nematocerous fly, and a slender filament which arises from the distal end of the last segment, and projects in line with it; this filament, the homologue of the arista, is termed the ***style***. The complex antenna of the Muscid flies has, in fact, been evolved from the simple Nematocerous antenna by a concentration of the basal joints and an elongation of the distal. The relation of this change in form to the function of the parts has been discussed by Townsend. According to this authority, the sense pits in the terminal joint of the scape are olfactory organs, and it is on account of the high degree of development of the olfactory sense that the third antennal joint has become so greatly enlarged, and has, so to speak, grown away from the rest of the organ. The function of the arista is to act as a sensory and tactile organ, for the protection of the very highly specialized third joint, by giving warning to the fly when it approaches obstacles. He suggests an interesting relation between the plumosity and the joints of the arista. In those forms in which the arista is plumed only on one side, the hairs are numerous and complex (cp. *Glossina*), and the small joint between the arista and the scape is not well developed, the arista appearing to arise directly from the scape and to be capable of little or no movement. On the other hand, in those forms in which the arista is feathered on both sides the hairs are generally simple and comparatively few in number, while the joint between the arista and the scape is well developed, and is obviously capable of free movement. The range of movement of the arista will thus counterbalance the paucity of the sensory hairs, and a fly with a stationary arista, but with a complex arrangement of sensory hairs, is as well equipped as one with few hairs, but a wide range of movement.

In the Pupipara the antennae are very much reduced, and are a little difficult to recognize. The scape consists of a single joint, roughly oval in shape, and enclosed in a deep chitinous pit on the surface of the head capsule, from which it can be partially protruded by the action of certain muscles attached at its base. There is no arista like that of the Muscid flies, but at the tip of the scape there are several stout forwardly directed bristles which probably represent it. The antennae and the pit in which they lie are of the same leathery consistence as the rest of the integument.

THE MOUTH PARTS AND SUCKING APPARATUS

It is characteristic of the Diptera that the mouth parts are adapted for sucking, and in the blood-sucking forms they are also modified to form a piercing organ. As it is through the mouth that all blood parasites must pass, either to or from the host, a detailed consideration of the region, and of the mechanism by which the parts act, is necessary. As a matter of convenience the first part of the alimentary canal, which is modified to form the sucking apparatus, will also be described here, for it is so intimately connected with the mouth parts both in function and in structure that the two cannot be satisfactorily considered separately.

The mouth parts project beyond the head, and form a more or less cylindrical bundle, termed the proboscis. Its shape, relative length, and the position in which it is held, are of importance in systematic work. It may be cylindrical and of approximately the same diameter throughout, as in the mosquitoes, or swollen at the base and pointed distally, as in *Stomoxys*; or cylindrical and thick with a joint in the middle, as in the house fly and its near allies. It may be short and inconspicuous, as in *Simulium* and *Ceratopogon*, or very long, as in many mosquitoes. The position in which it is held varies from the horizontal to the vertical, as, for instance, in the Anopheline mosquitos and the Tabanidae. It may be straight or curved. In the non-biting Muscid flies, and in the genus *Philaematomyia*, it is completely retractile; in *Stomoxys* and in *Glossina* only partially so. In *Hippobosca* almost the whole of the proboscis can be withdrawn within the head.

The constituent parts of the proboscis, excluding the wall of the head capsule when it takes part, are enumerated as follows:—

The Labrum, or upper lip.
The Epipharynx, usually combined with the labrum.
The Hypopharynx.
The Mandibles, appendages of the fourth segment of the head.
The First Maxillae, appendages of the fifth segment.
The Labium, or lower lip, composed of the appendages of the sixth segment, fused together except at their distal ends.

Of these, the mandibles may be entirely absent, and the first maxillae may be represented only by their palps. In the higher Diptera a portion of the wall of the head capsule may be evaginated to form a part of the proboscis, using the term in its widest sense.

The Dipterous mouth, highly specialized as it is, is but a modification of the arthropod mouth for a special mode of life, and to understand its structure and mechanism it is necessary to compare it with less differentiated forms. The mouth in the Arthropoda is typically a biting one, and is furnished with cutting jaws, the appendages of the head segments, with which the animal seizes and tears up its food. The jaws in the simplest forms are typical jointed appendages, and the mouth is adapted for the reception of solid particles. It will simplify the conception of the structure and mechanism of the Dipterous mouth if it is remembered that the organs which are used by even the most highly specialized forms are homologous with the cutting and clasping appendages used by the primitive insects to obtain their solid food.

Mouth parts of the cockroach

The common cockroach, *Periplaneta orientalis*, may be taken as an example of an insect with simple mouth parts; reference to the admirable account of this insect by Miall and Denny has already been made. The figures on Plate IV are taken from their book. In the cockroach all three pairs of appendages can be readily identified; they all function as cutting or clasping weapons, and the second and third are typical jointed arthropod appendages. The mandibles, like those of the Diptera, are the least typical, and have only one joint, that by which they are attached to the head; the point of attachment is termed the *ginglymus*. By means of its muscles the blade of the mandible can be moved in a transverse plane, till it comes in contact with its fellow of the opposite side. The maxillae are more complex, and consist of a number of joints. These are as follows: two basal joints, the *cardo* and the *stipes*, and three distal joints, arising about the same level from the stipes, and termed from within outwards the *lacinia*, the *galea*, and the *palp*. The shape and disposition of these parts is sufficiently indicated in the figures. As will be seen later, the maxilla in the Diptera retains the original form to a remarkable degree. The palp, for instance, is jointed in all but the highest forms, and retains its sensory character throughout.

The second maxillae lie behind the first, and form the posterior boundary of the mouth. They are fused together except at their distal ends, and are continuous posteriorly with a membrane which occupies the inferior surface of the head, and merges with that of the neck. It is in

PLATE III

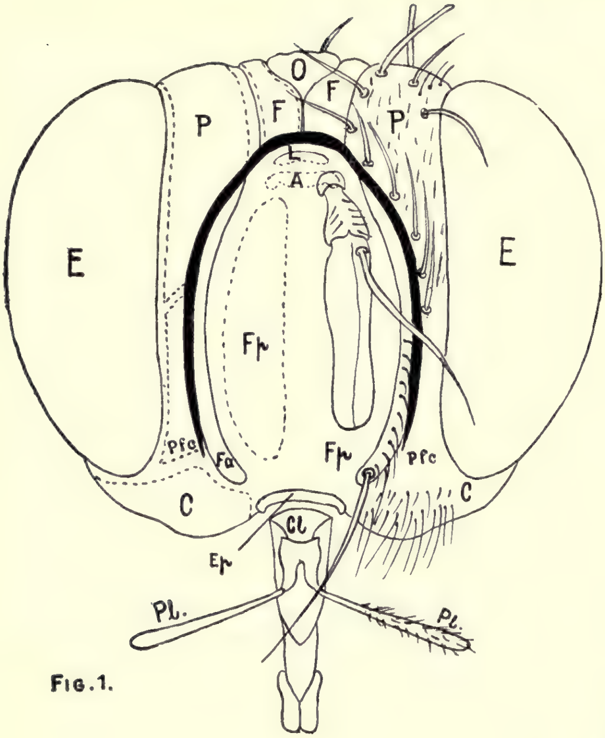
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FIG. 1.

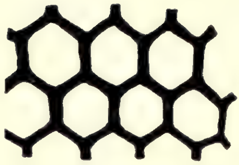

FIG. 2.

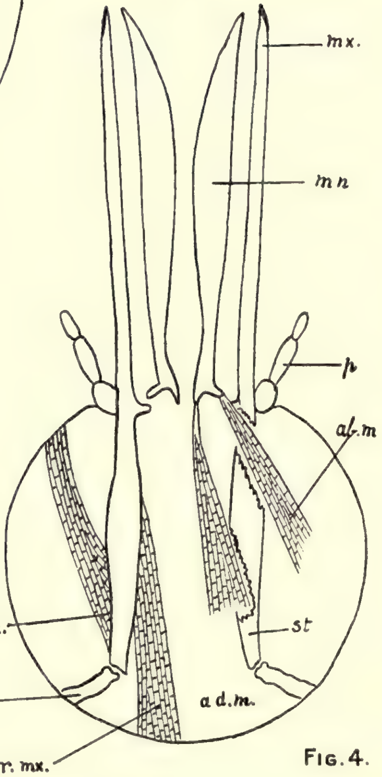
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FIG. 4.

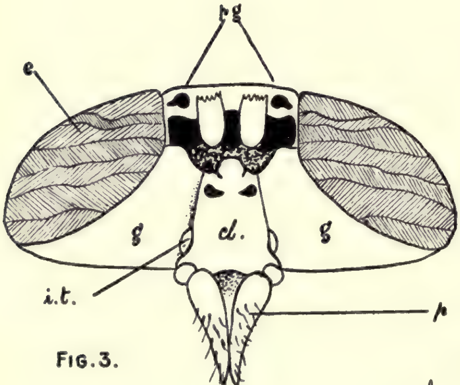
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FIG. 3.

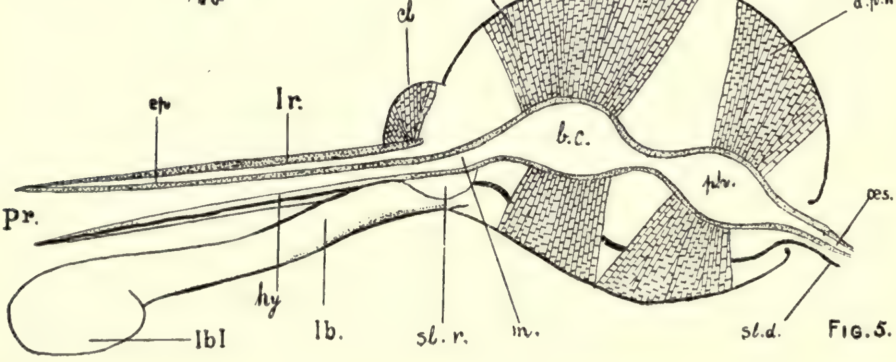
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FIG. 5.

PLATE III

Figure 1.	Front view of head of Muscoidean fly, (half in diagram) much enlarged. The heavy black line indicates the ptilinal suture. O = Ocellar plate. FF = Frontalia. PP = Parafrontals. Pfc = Parafacials. CC = Cheeks. EE = Compound eyes. L = Lunula (postfront of larval insects). A = Antennal ridge (mesofront of larval insects). Fp = Mesofacial plates (plus facialia equals prefront of larval insects). Fa Fa = Facialia. (Parts from lunula to facialia both inclusive taken together constitute the front of larval insects). Ep = Epistoma. Cl = Clypeus. Pl Pl = Palpi. Copied, with the above description, from Townsend.
Figure 2.	The facets of the compound eye of *Tabanus.*
Figure 3.	The head of *Haematopota pluvialis,* ♀ seen from the front. pg., pigment spots. These are of frequent occurrence in the Tabanidae, and are useful in distinguishing species. This is an example of a dichoptic fly.
Figure 4.	Scheme of the mouth parts in the Orthorraphic Diptera. Observe the abductor and adductor muscles of the mandible, ab.m. and ad.m., and the protractor and retractor muscles of the maxilla, p.mx. and r.mx.
Figure 5.	Scheme of the sucking apparatus in the Orthorraphic Diptera.

consequence somewhat difficult to decide how much of the labium is properly to be regarded as composed of the appendages. The two basal pieces are known as the *submentum* and the *mentum*. The latter is conspicuous in the elongate proboscis of the Diptera.

The mesial constituents of the mouth apparatus are inconspicuous in the cockroach. The labrum is a small transverse flap which occupies the space between the mandibles in front, and is attached to the clypeus by a moveable joint. It is, in fact, a process of the clypeus, and forms the dorsal boundary of the mouth aperture. There is no epipharynx in the cockroach, and the hypopharynx is represented by a small chitinous fold in the floor of the mouth, on the posterior surface of which the salivary duct opens.

Main features of the proboscis in the Diptera

Now it is from such a condition of affairs, both as regards structure and function, that the Dipterous mouth has evolved, and from a consideration of the change in habit one can deduce the changes which would become necessary in the structure of the parts, firstly, in consequence of the exchange of solid food for fluid, and secondly, in the case of the blood-sucking forms, as a result of the necessity for making a wound in the skin of the host. For the first a tubular channel up which the fluid can be sucked is essential, for the mouth parts of such insects as the cockroach are adapted only for the ingestion of solid particles. In the Diptera this is accomplished by the development, to a very high degree, of just those parts of the mouth apparatus which are rudimentary in the cockroach, namely, the epipharynx and the hypopharynx. (Plate III, fig. 5.) These are outgrowths, from the dorsal and ventral walls respectively, of the stomodaeum,* which pass forward to the level of the terminations of the other appendages; the dorsal outgrowth is deeply grooved on its under surface, and the ventral one flattened, the two being so apposed to one another as to form a closed channel. The hypopharynx fulfils the secondary but equally essential function of conveying the saliva to the level of the distal orifice of the channel, in order that it may be mixed with the food. The labrum, which lies immediately above the epipharynx, is produced forwards and partially fused with it in order to strengthen the channel. The muscle at the base of the labrum, which in the cockroach lifts up the labrum in order to widen the mouth, is retained, and functions in regulating the size of the distal aperture between the epipharynx and the hypopharynx.

To save confusion in the subsequent descriptions, the point at which the epipharynx and the hypopharynx separate from the stomodaeum may be termed the *mouth*. The distal aperture between the epipharynx and the hypopharynx is the *prestomum*.

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* The first part of the alimentary canal. See page 26.

In addition to a channel by which the fluid food can be conveyed to the mouth, some apparatus is necessary to provide a sucking force. This is formed by a modification of the stomodaeum within the head. The walls of this are strongly chitinized, and are provided with muscles which pass between them and the walls of the head capsule; on contraction these muscles draw the walls of the tube apart and so produce a negative pressure. This causes the fluid to flow up the food channel.

The appendages are modified for their specialized function in the blood-sucking forms by elongation, by the reduction of superfluous parts, and by the development of a suitable armature. (Plate III, fig. 4.) In the simpler forms, such as the mosquitoes and the horse flies, the wound is made by the mandibles and the first maxillae, the labium serving mainly as a sheath for the other appendages and the food channel. They are specialized into piercing stylets, elongated on account of the depth of skin which has to be pierced in order to reach to the level of blood; the number of joints, in the case of the maxilla, is reduced to ensure rigidity, and the armature and musculature are so modified as to be suitable for making a deep wound of narrow bore. In the higher Diptera the mandibles and first maxillae are not present, and the whole function of making the wound is transferred to the second maxillae, at the distal end of which there is developed a highly specialized arrangement of teeth.

Considered with regard to their mouth parts, the blood-sucking Diptera fall into two well-defined classes, those in which the mandibles and first maxillae are present and functional, and those in which they are absent, and their function fulfilled by the second maxillae. These two classes correspond with the two sub-orders into which the Diptera are divided, the Orthorrapha and the Cyclorrapha. Some examples of each will now be described in detail.

The proboscis of *Tabanus* and of the allied genera (excluding *Pangonia*) is relatively short, and hangs downwards from the lower surface of the head. All the parts enumerated at the commencement of this section are present and functional.

Tabanus

The *mandibles* (Plate IV, fig. 4) are broad flat blades of yellow chitin, slightly recurved on their inner edges. The cutting armature is limited to the distal portion of the inner edge, and consists of a row of extremely fine serrations like those

PLATE IV.

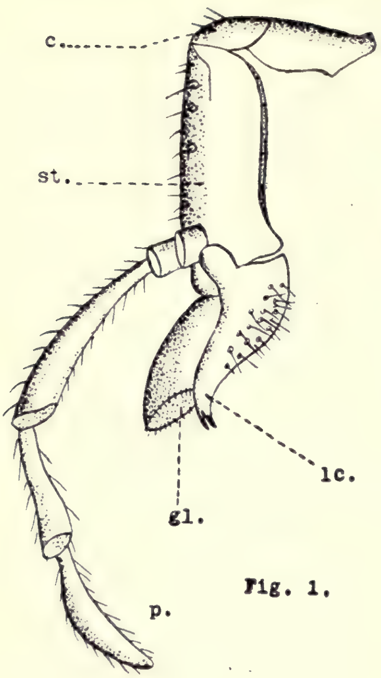


Fig. 1.

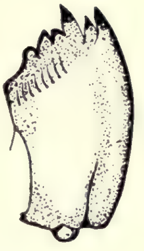


Fig. 2.

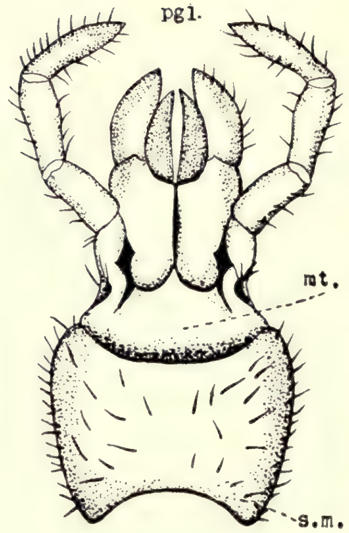
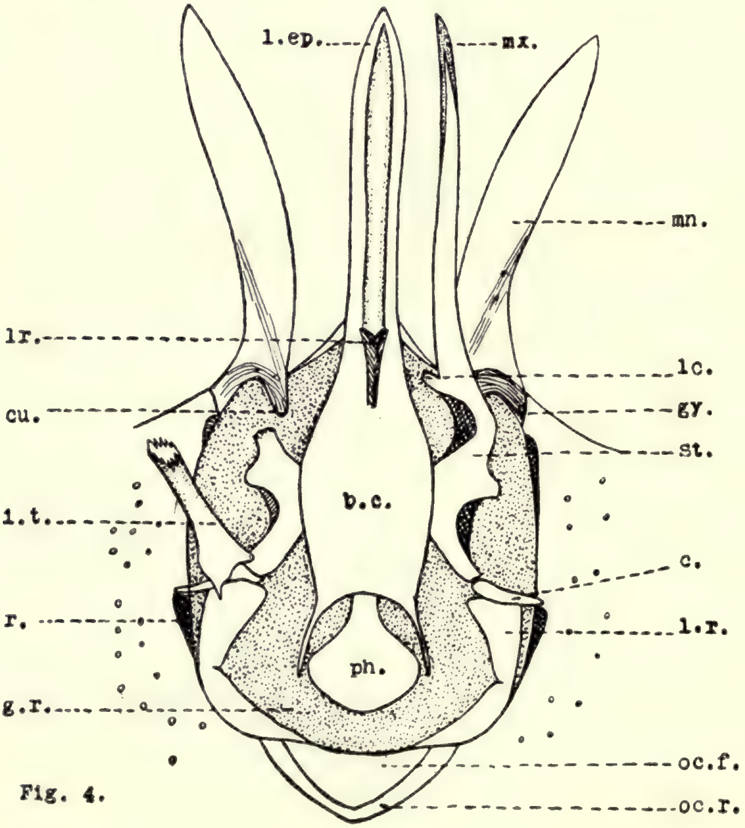


Fig. 3.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oc.r.

Fig. 4.

PLATE IV

Figure 1. The first maxilla of the cockroach. × 20

Figure 2. The mandible of the cockroach. × 20

Figure 3. The second maxillae of the cockroach. pgl., paraglossae. × 20. These three figures from Miall and Denny.

Figure 4. The mouth parts of *Haematopota pluvialis*, as displayed by cutting off the upper and anterior part of the head capsule. The blade of the maxilla is omitted on the left side, and the palps are not drawn. The intracranial tunnel of the left side is shown, broken from its attachment to the anterior wall of the head. gy., ginglymus, the joint of the mandible. l.r., a strong flattened rod of chitin, which supports the intracranial tunnel at its base, and compensates for the laxity of the wall in the gular region, g.r., where the chitin is replaced by membrane. The presence of this strong bar is easily recognized in dissection. r., the ridge on which the cardo rests. cu., the cornu of the mandible, to which the strong adductor muscle is attached. oc.r., a ridge of thick chitin surrounding the occipital foramen. × 65.

on a hand saw. The outer edge of the blade is thickened from the point upwards, and the inner in its proximal half; at the base the mandible is divided into two strong cornua, the internal one of which is free, the external being articulated to the epicranium at a prominent angle. The muscles of the appendage arise in the floor of the head cavity, and are inserted into the two cornua; those which pass to the internal cornua are the strongest, and act as adductors; those inserted into the external cornua act as abductors.

The *first maxillae* (Plate IV, fig. 4 and Plate V, fig. 4), as is the case in the cockroach, are more complex than the mandibles. Although the appendage is, of course, altered in form for its specialized function, all the parts seen in the simpler insects are present. The blade, which corresponds to the galea of the cockroach, is a stout chitinous rod, quadrilateral in section in its distal part, but flattened towards the base. It is armed with stout rasp-like teeth, set closely together in an imbricate manner, on the whole of the surface of the distal end, and for some distance on the inner side. All these teeth point towards the base of the blade. The blade is directly continuous at its base with a much convoluted piece of chitin, the *stipes*, which runs across the floor of the head at the side of the buccal cavity, and is attached to the wall a little in front of the occipital foramen by the interposition of a short stout wedge-shaped rod, the *cardo*. The lacinia is represented only by a short peg-shaped projection on the inner side of the base of the blade. The *palp* is well developed. It consists of two joints, a short cylindrical one and a larger conical one. The two palps turn a little forward from their origin, and converge towards one another in front of the proboscis, so as to conceal its upper part when looked at from the front. When the fly is feeding they are directed forwards, away from the proboscis.

The muscles of the maxilla are arranged in two sets, one of which protracts the blade, while the other retracts it. The protractor fibres arise from the anterior wall of the head capsule, and pass backwards to be inserted into the stipes; the retractors, which are much stronger, run in the opposite direction, from the neighbourhood of the occipital foramen.

The method by which these appendages act in the making of the wound will now be evident. The mandibles are rotated inwards on their point of attachment to the head capsule by their adductor muscles, and the blades are thus drawn obliquely across the tissues. They are replaced in position by the abductors. The maxillae are alternately protracted and retracted by two sets of muscles pulling in different directions, and at each retraction the barb-like teeth are drawn through the tissues. In each case the armature of the blade and the musculature are admirably adapted to one another. One might compare the action of the mandible to that of a circular saw cutting through a short arc, and that of the maxilla to a file, thrust in and out of the wound. As the wound is deepened the cutting blades are gradually lowered into it. (Plate IV, fig. 4.)

The *labrum-epipharynx* has its two constituent parts fused together to form a flattened spatulate slip, convex on its dorsal surface, and resembling a two-handed sword when seen from the front. The labral lamina is thinner than the epipharynx, and does not reach quite to the distal end. The two are only loosely united at the proximal end, where the labrum is attached to the clypeus by a short tongue-shaped piece, in which is inserted a short muscle. The epipharynx is separated from the labrum by a small amount of cellular tissue, and at the upper end it fuses with the dorsal plate of the buccal cavity, there being no suture to break the continuity of the chitin. Its distal end is blunt, and has on it three sets of minute tubercles, two lateral and one median. These are not cutting teeth, but have another function, which will be referred to later· The ventral surface is strongly concave, and forms the dorsal wall of the food channel.

The *hypopharynx* resembles the labrum-epipharynx in shape, but is much thinner and more slender, and is produced to a narrower point; the extreme tip, in fact, is very soft and thin. It is a little shorter than the labrum-epipharynx, and flatter on section. When the parts are *in sitû* it closes in the gap between the two lateral edges of the groove in the epipharynx. At its base the hypopharynx is directly continuous with the ventral plate of the buccal cavity. It is pierced throughout its length by the salivary duct. Where it merges with the buccal cavity there is a small chitinous pouch, the salivary pump, on the ventral surface. (Plate V, fig. 1.) This is interposed between the salivary duct in the head and that in the hypopharynx, and is surrounded by a small fan-shaped muscle, by which the supply of saliva to the wound is believed to be regulated. (Plate V, fig. 3.)

The *labium*, unlike the other mouth parts, is a soft organ, and has a wall composed of thin plates of chitin and membrane, enclosing a series of muscles and other structures. It and the palps are the only parts which can be seen on external examination, the other organs being entirely concealed in a groove on its anterior surface when the proboscis is in the position of rest. It is divided in its distal third into two labella. The wall of the labium proper is formed, on the posterior and lateral aspects, by a shield-shaped plate of chitin, the *mentum*; anteriorly there is a thin gutter-shaped plate which may be termed the *labial gutter*, in which the piercing parts rest. These two plates are connected together by a loose membrane passing between their lateral edges. The *labella* are bilaterally symmetrical oval lobes, continuous with one another posteriorly, but diverging in front. Their external walls, continuous with the walls of the labium, are strengthened along the distal border by thin plates of chitin, the proximal one of which is indented to receive a prominent spur of the mentum, the two forming a loose joint. The internal walls of the labella, which are normally in contact with one another, are formed by a complex structure known as the *pseudotracheal membrane*, by means of which the fly is enabled to absorb fluid from moist surfaces. This structure, which is of common occurrence in the Diptera, will be described in detail as it occurs in *Musca*, and it will be sufficient to note here that its occurrence in *Tabanus* is in accordance with the observation often made, that these flies can drink water.

The muscles of the labium lie within the cavity enclosed by the wall, and serve to control the position of the labella. They arise in three sets from the internal surface of the mentum, and are inserted into the internal surfaces of the chitinous plates of the labella. When all three sets contract at the same time the labella are diverged from one another, and also retracted ; by means of the anterior and posterior sets the fly is able to adjust the oral surfaces to the surface on which it wishes to feed. Retraction of the whole of the labella takes place when the piercing stylets are introduced into the wound ; the intrinsic muscles are assisted in retraction by a smaller pair inserted into two conspicuous cornua at the proximal end of the mentum.

When the internal or oral surfaces of the labella are to be used for the absorption of fluid from a moist surface, the space between the inner and outer walls of the organ is distended with blood forced down from the head and body of the fly by respiratory movements. The details of this important mechanism will be discussed with regard to *Musca*, but it is well to note that, in the case of *Tabanus* and in fact all the Diptera, the space enclosed by the labellar walls is continuous with the general body cavity.

In the space between the inner and outer walls of the labella there is a labial salivary gland, which resembles that of *Musca*, and need not be described here on that account.

The channel between the epipharynx and the hypopharynx leads into

The Sucking Apparatus

the pumping apparatus, by means of which the blood is drawn up from the wound. It has already been stated that this is developed from a part of the alimentary tract within the head. To understand the true nature of the pumping organ it is necessary to refer for a moment to the embryology of the parts. The alimentary tract of insects is developed in three divisions, only the middle one of which is lined with true digestive epithelium. The anterior and posterior regions are formed by invaginations of the cuticle and are therefore lined with chitin which is continuous with that of the exo-skeleton. In most parts this chitin forms only a thin layer, but in a part of the canal within the head the walls are strongly chitinized to form the sucking chamber. It may be supposed that in the earliest forms the whole of the tube was dilated to form a single chamber, and united with the wall of the head capsule by means of radiating muscle fibres, which, by drawing the walls apart, could produce a negative pressure sufficient to draw up the fluid. In the course of the differentiation of species the single cavity became divided into two, of equal or unequal size, and a sphincter muscle, in some cases, developed between them. (Plate III, fig. 5.)

In all the Diptera these two chambers, in one form or another, can be distinguished, and we may adopt for them the terms *buccal cavity* and *pharynx* respectively. The original circular lumen is modified, in the part which functions as a pump, by the moulding of the wall into two, or in some cases three, strong chitinous plates, normally in contact with one another but capable of being pulled apart by the dilator muscles. In the Orthorrapha there are two functional pumps, while in the Cyclorrapha the first is modified to form a connecting tube, without dilator muscles.

In *Tabanus* the two pumps are well developed. (Plate V, fig. 1.) The buccal cavity is an oblong chamber composed of two flattened plates of chitin, continuous, as previously stated, with the epipharynx and hypopharynx of the food channel. At the posterior or upper end the walls are produced into two stout cornua, between which the cavity opens into the pharynx by a short and narrow channel surrounded by a sphincter muscle. The buccal cavity, being in line with the food channel, is perpendicular to the long axis of the body, while the pharynx is in line with it, the channel between them opening into its middle portion. It is formed by a single quadrilateral plate of chitin, the lateral angles of which are turned downwards and connected with one another by a membrane continuous with that of the channel leading from the buccal

PLATE V

Figure 1. The sucking apparatus of *Tabanus*, schematic, in profile. e.b.c., a muscle with a fine tendon, attached to the cornua of the buccal cavity on each side. These probably draw up the cavity, and with it the epipharynx and the hypopharynx, while the mandibles and maxillae are in action. sph., sphincter muscle. c.p., compressor muscles, which assist in returning the walls of the pharynx to a position of rest. e.l., elevator muscle of the labrum, by which the size of the prestomal opening is regulated. p.ph., protractor muscles of the buccal cavity, acting probably in opposition to e.b.c. r.œs., retractor muscle of the œsophagus. Note that the pharynx is anterior to the brain, while in the mosquito it is mainly posterior. × 40 about.

Figure 2. Transverse section through the head of a mosquito, to show the arrangement of the plates of the pharynx. l.d.ph., the lateral dilators.

Figure 3. The labium of *Haematopota*, seen in profile, in a cleared preparation. a.g., the groove in the anterior surface in which the piercing stylets are concealed. The membrane, mb., is continuous with that of the gular region. × 54.

Figure 4. The distal end of the maxilla of *Tabanus*, to show the teeth. × 650.

Figure 5. The sucking apparatus of *Joblotia*, a large mosquito. f.c., a flange projecting inwards under cover of the clypeus, to which is attached a muscle, mu., probably regulating the size of the prestomal slit in the act of sucking, by lifting up the labrum. t., the chitinous tube which passes through the brain and connects the buccal cavity and the pharynx. f., a chitinous flange providing attachment for the muscle which works the salivary pump. × 90.

PLATE V.

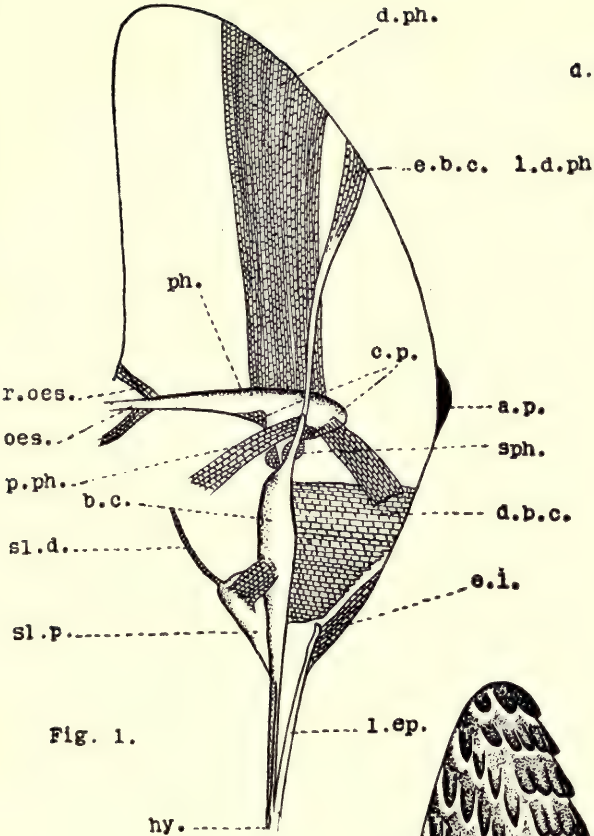
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Fig. 1.

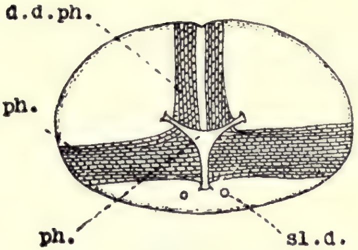
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Fig. 2.

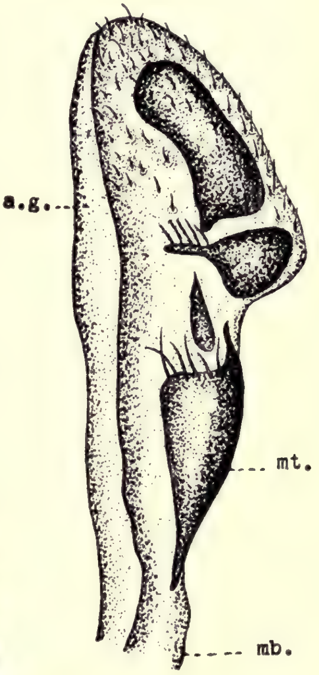

Fig. 3.

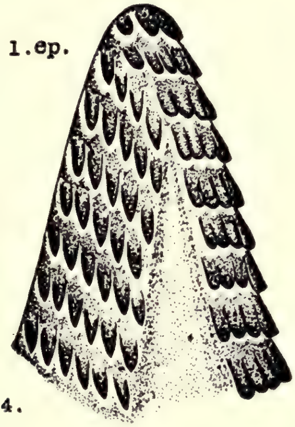

Fig. 4.

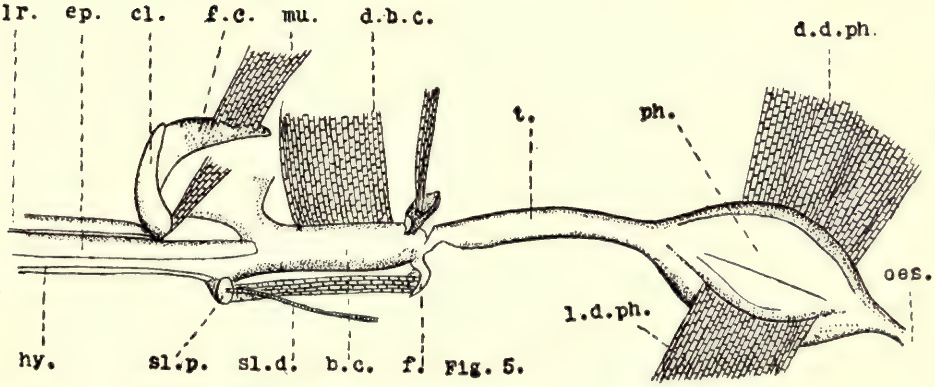
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Fig. 5.

cavity, and with the oesophagus, which opens out of the posterior end of the pharynx. The muscles which dilate these chambers arise from the walls of the head capsule. Those of the buccal cavity are inserted into the anterior surface of the dorsal plate, and arise from the epicranium below the antennae. Those which dilate the pharynx arise from the region of the vertex, and pass down to the dorsal surface of the pharynx; there are some subsidiary muscles attached to the turned down angles of the plate, arising in the lateral regions.

The blood is pumped up, not by a single dilatation of the chambers, but by rapidly repeated ones, and the mechanism by which the plates are brought again into contact with one another in readiness for the next contraction has now to be considered. It has been repeatedly stated, with reference to the similar structure in the mosquito, that the replacement of the plates is brought about by the natural elasticity of the chitin, but the process is more complex than this. The true explanation of the collapse of the chambers is to be found in the presence of certain large and tough air sacs, which surround the brain and take up a large proportion of the space within the head capsule; these are in communication with the rest of the respiratory system of the fly. When the sucking pumps are dilated, room must be made in some manner for the increased contents of the head, and air is either forced out of these sacs into the thorax, or else the air in the sacs is compressed. When the cavity is to be emptied again, the air is either returned from the body to the sacs by means of the contractions of the muscles of the body wall, acting as in respiration, or else the positive pressure in the air sacs becomes active as soon as the contractions of the muscle pass off. With the collapse of the chamber the blood in the cavity passes backwards to the pharynx, or from the pharynx to the oesophagus.

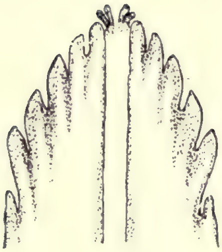
The mechanism of the mouth parts and sucking apparatus in *Tabanus* may be summed up as follows. The fly settles down on the skin of the host, and by means of the tactile hairs on the end of the proboscis selects a suitable place. A firm hold is then taken on the skin by means of the claws on the feet, the labella are retracted to expose the piercing stylets, and are also diverged from one another so that their oral surfaces are applied to the skin. The mandibles and maxillae are then put in action, the former acting like a saw and the latter like a file, and by rapidly repeated movements cut a hole in the skin. Meanwhile the epipharynx and hypopharynx are drawn slightly upwards, by means of a pair of muscles which pass from the cornua of the buccal cavity to the epicranial wall in the region of the vertex. When the level of blood is reached they are protracted. The pumping action in the buccal cavity then commences, the sphincter separating it from the pharynx being contracted. Immediately the cavity is full the sphincter relaxes, and the pharynx dilates as the blood is sucked into it from the first chamber. When the air pressure is in turn exercised on the pharynx the blood flows into the oesophagus.

Other Orthorraphic Diptera—Plate VI

The other blood-sucking Orthorrapha, with the exception of the mosquito, which will be dealt with separately, resemble *Tabanus* in the structure of their mouth parts, the differences being only in matters of detail. In all the proboscis is relatively short, and is directed downwards from the under surface of the head. The labium functions merely as a sheath for the other mouth parts, none of these forms having a pseudotracheal membrane like that of *Tabanus*. The mandibles are in each case flat and blade-like, with a serrated internal edge. The serrations may, as in *Simulium*, (fig. 6), be continued for a short distance on to the external margin, so that the blade cuts in abduction as well as in adduction. The maxilla in *Simulium* (fig. 6) is flattened and shaped like a long and narrow triangle, with a simple armature consisting of a single row of strong recurved teeth down each edge. The blade will, therefore, cut only in retraction. In *Ceratopogon* the maxilla is stout at the base, but attenuated and pointed at the distal end, where it is armed with a row of five fine hook-like teeth, set on the inner and thinnest edge. The maxilla of *Phlebotomus* (fig. 7) is stout and rod-like, and has an armature on two sides. On one side—it is difficult to say which, for the blade is very easily twisted—there is a row of minute but stout teeth extending from the distal extremity for a short distance, and on the other a short row of much smaller teeth commencing some distance from the tip. The first set point towards the base of the blade and will, therefore, cut during retraction; the second set point towards the tip and cut only in protraction. In each case the blade of the maxilla becomes continuous at its base with the stipes, and is provided with retractor and protractor muscles, of which the former are always the stronger.

In these three forms the distal ends of the labrum-epipharynx and the hypopharynx are modified in a highly suggestive manner. The opening at the prestomum is in each case a transverse slit, for the distal ends are always flattened and the canal between the two parts broadened out. In *Simulium* (figs. 14 and 15) the end of the labrum-epipharynx is broad, soft, and membraneous, and has on it two minute sets of three curved hooks; on the dorsal aspect there is a row of stout and long but only

PLATE. VI.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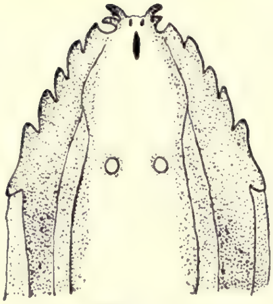
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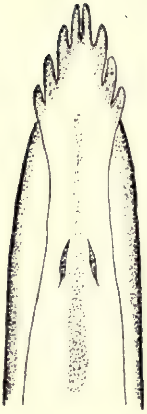
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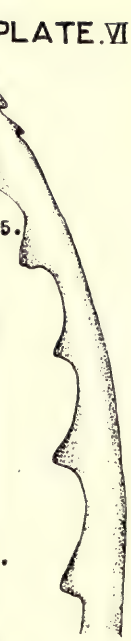
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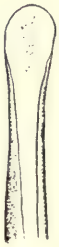
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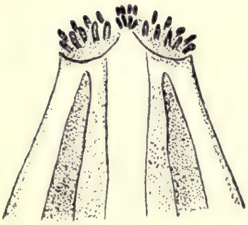
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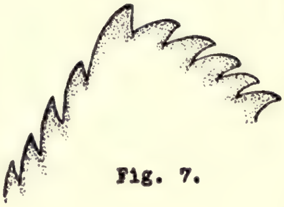
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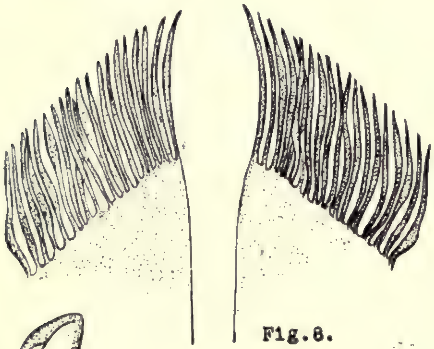
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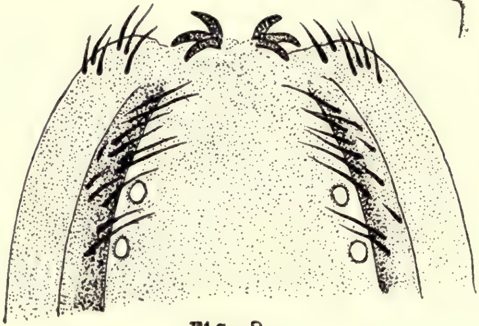
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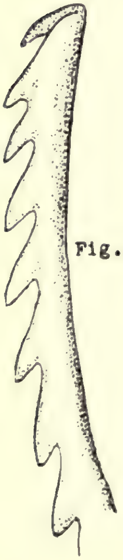
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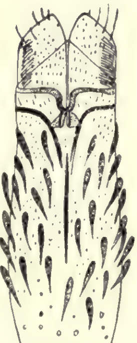
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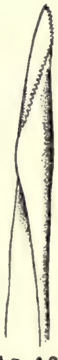
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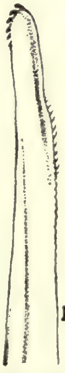


Fig. 13.

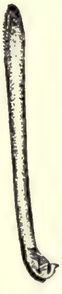


Fig. 14

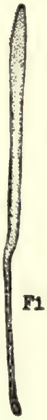


Fig. 15.

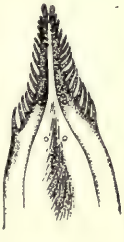


Fig. 16.

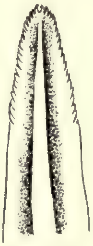


Fig. 17.

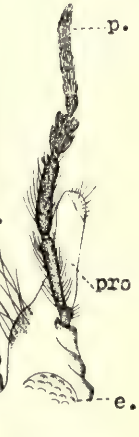


Fig. 18.

PLATE VI

Figure 1. The hypopharynx of *Ceratopogon sp.* × 1200

Figure 2. The labrum-epipharynx of same. × 1200

Figure 3. The labrum-epipharynx of *Joblotia sp.* Very highly magnified.

Figure 4. The hypopharynx of same. Very highly magnified.

Figure 5. The maxilla of same. × 630

Figure 6. The labrum-epipharynx of *Tabanus albimedius*, dorsal view. × 600

Figure 7. The cutting edge of the mandible of *Simulium indicum.* × 1000

Figure 8. The hypopharynx of same. × 630

Figure 9. The labrum-epipharynx of same. The lateral hairs are very much finer than represented in the drawing. × 630

Figure 10. The maxilla of same, side view. × 1000

Figure 11. The labium of *Phlebotomus papatasi*, seen from behind.

Figure 12. The mandible of same, distal end.

Figure 13. The maxilla of same, showing the two sets of teeth.

Figure 14. The mandible of same.

Figure 15. The maxilla of same, showing the 'apodeme,' or representative of the stipes.

Figure 16. The labrum-epipharynx of same.

Figure 17. The hypopharynx of same.

Figure 18. The head of same in side view, showing the proboscis, pro., and the long palp.

Except in figures 11, 15, and 18, only the distal ends are shown. Figures 11 to 18 are from Grassi, copied by Mr. G. Taylor.

faintly pigmented hairs, on each side of the canal. The distal border of the hypopharynx is split up into a row of innumerable elongate processes, which give it the appearance of a frayed piece of cloth. In *Ceratopogon* (figs. 1 and 2) both organs have indented margins, with five processes produced distally between the notches ; the labrum-epipharynx is the broader organ of the two, so that its processes overlap those of the hypopharynx.

In *Phlebotomus* the two parts of the food canal are more pointed at their distal ends. The borders of both are split up into fine tooth-like processes, those on the hypopharynx being much smaller and more numerous than those on the epipharynx. The significance of these 'teeth' will be discussed when the parts in the mosquito have been described.

In each of the above flies the two sucking chambers are well developed and functional. In *Simulium* the buccal cavity is like that of *Tabanus,* while the pharynx is composed of three plates, like that of the mosquito. The two are, as in *Tabanus,* placed perpendicular to one another. In *Ceratopogon* the buccal cavity is also composed of two plates, dorsal and ventral, but it is smaller, and does not appear to take as much part in the sucking operation as the pharynx ; this is also composed of two plates, and resembles the buccal cavity, to which it is inclined at about half a right angle. In *Phlebotomus* the buccal cavity, which resembles that of the others, is small; the pharynx is the more important sucking chamber, and is composed of three chitinous plates.

The mosquito represents an extreme type, characterized by great elongation of the mouth parts, reduction in the size of the buccal cavity, and a corresponding increase in the size of the pharynx. The elongation of the mouth parts is accompanied by a reduction in the transverse diameter, specially noticeable in the labium.

The Mosquito—Plate VII

In the Anopheline mosquitoes the proboscis is held straight in front of the head in the position of rest, while in the other genera it is inclined downwards. The position in which it is held in the act of feeding is, however, the same in the two forms, namely, perpendicular to the long axis of the body, or nearly so.

The *mandibles* (figs. 1 and 3) are extremely slender slips of chitin, armed only at their distal ends. In sections the blade appears concave on its inner surface, and is closely pressed against the hypopharynx. At the tip, in the case of *Anopheles,* the blade is broadened out a little, and has a short row of extremely fine serrations. In many species of *Culex* the teeth on the mandible cannot be distinguished at all. At the base the blade is broader and stouter, and turns sharply outwards at its articulation with the head; the muscles attached to it are small, and the mandible does not appear to play an important part in the cutting operation. Mandibles are absent in the male, and the whole appendage may be regarded as a retrogressing one.

The *maxillae* (figs. 1 and 2), slender though they are, are stouter than the mandibles. On section the two blades are seen to form a concavity on which the hypopharynx rests. When mounted flat the blade is seen to have one edge thick and rounded, and the other extremely sharp and attenuated; the surface between the two edges is divided into a number of separate areas by means of transverse lines, which produce slight indentations where they meet the thinner edge. At the distal end there is a single row of short conical teeth, arising from the thin edge. The number of these differs in different species, but is usually from ten to twenty. At the base the blade merges into the stipes, which has often been described as the 'apodeme' of the maxilla. The retractor muscles attached to it are much more powerful than the protractors. The palps, which vary in length and in the number of joints in the different genera, and are of importance in classification, are attached to the base of the blade where it merges with the stipes; as in the other forms, they are held out in front, away from the proboscis, when the mosquito is feeding.

In some of the larger mosquitoes the blade has a much more formidable cutting apparatus than the one just described. In a species of *Joblotia* (fig. 7) there are three sets of teeth. One set resembles that seen in *Anopheles*, and does not extend quite to the tip of the blade; these teeth are only slightly recurved, and can probably cut in both directions, though most efficiently in retraction. Distal to them and on the same border there is a row of much finer and sharper teeth, which point towards the tip, while at the extreme end of the blade, distal to the others, there is a row of stout but minute teeth like those on the maxilla of *Tabanus*, extending on to both surfaces of the blade. Such a weapon will cut both in protraction and in retraction.

The *labrum-epipharynx* is not flattened as in the other forms, but rounded. The constituent parts are more closely fused together, and there is very little loose tissue between them. The epipharynx takes the greater part in the formation of the stylet, and is produced beyond the labrum. The distal end(Plate VI, fig. 3) is in most genera obliquely truncated in such a manner as to resemble a J pen, and is incised in the longitudinal direction, the portions of the margin between the incisions projecting as minute 'teeth'. There is usually a well marked central split. At the base the epipharynx and the labrum separate, the former fusing with the buccal cavity, the latter projecting within the cavity of the clypeus, which in the mosquito is always prominent.

The *hypopharynx* (figs. 1 and 4) is an extremely delicate flattened slip, perforated throughout its length by the salivary duct. It falls a little short of the other mouth parts, and has a soft distal end. (Plate VI, fig. 11.)

The *labium* (fig. 1, and Plate VI, fig. 4) is a long, narrow, and flexible chitinous tube, hollowed out on its anterior surface for the reception of the piercing parts. The greater part of its wall is formed by the mentum, which forms the posterior and lateral sides, and arches inwards across the groove. The anterior surface is completed by membrane, forming a labial gutter which is depressed below the lateral margins. In the space enclosed by the mentum and the labial gutter there are several muscles, some tracheae, and a few free cells; some of the latter belong to the haematocoele, for the cavity of the labium is in communication with the rest of the body cavity. At its distal end the labium is divided into two small labella, which are articulated to the rest of the organ by a definite joint formed by small chitinous rods. The distal margin of the labellum has on it many fine sensory hairs. There is no pseudotracheal membrane, but delicate longitudinal grooves can be made out on the inner surfaces of the lobes. At the proximal end the wall of the labium becomes continuous with the membraneous area at the inferior surface of the head.

The movements of the labium are the same as those in *Tabanus*. The intrinsic muscles, which are easily seen in cross sections, are inserted partly into the chitinous rods which form the joint between the labium and the labella, and partly into the lower end of the mentum. When the insect commences to feed the labella are applied to the surface of the skin, and diverged from one another so that their oral surfaces are in contact with it. The piercing stylets are then thrust into the skin between the two labella, which act, to use Nuttall and Shipley's expression, like the fingers of a billiard player in guiding the cue. As the chitinous stylets enter the skin, the labium is bent backwards, the labella retaining their position. The bending is in consequence of the disproportion in the length between the labium and the free portion of the stylets, but it is not produced by mere mechanical displacement. The upper end of the mentum is not a uniform sheet of chitin, but is broken up into a number of minute elongate transverse plates set closely side by side, with membraneous interstices, an arrangement which enables it to bend readily when the muscles which traverse the labium in its long diameter contract. In a mosquito in the act of feeding the labrum-epipharynx can be distinguished with the aid of a lens, passing directly from the head into the wound, and widely separated from the labium, the upper part of which is bent sharply backwards.

The *sucking apparatus* of the mosquito (Plate V, fig. 5) differs from that of any of the flies so far considered in several important particulars. The first sucking chamber is very small, and takes only a minor part in the mechanism, while the pharynx is very well developed, the two being connected by a stout chitinous tube of considerable length, instead of a short membraneous duct. It should be noted that the pharynx of the mosquito is not, strictly speaking, homologous with that of *Tabanus*, for it is situated mainly behind the brain, instead of anterior to it. Their true relation will be evident from what has been said with regard to the development of the sucking chambers.

The buccal cavity lies below the clypeus, and commences by the fusion of the two edges of the groove in the epipharynx, the upper lamina of the hypopharynx uniting with the tube so formed; it terminates at the level of the posterior border of the clypeus, running upwards and backwards, not quite in line with the food channel. Its lumen is transverse in the anterior part, and circular posteriorly. The ventral wall is the thicker of the two, and is chitinous throughout. The dorsal wall is chitinous in front and behind, but has a membraneous area in the middle portion. The muscles which dilate the cavity are inserted into its dorsal wall, and arise from the internal aspect of the clypeus.

There is a curious structure, a part of the salivary apparatus, attached to the anterior end of the ventral plate of the buccal cavity. (Plate V, fig. 5.) It consists of a small cup-shaped receptacle, with the open end directed posteriorly, and covered by a tough membrane which is pierced in its centre by the salivary duct coming from the thorax. The closed anterior end communicates directly with the salivary duct in the hypopharynx. Where the duct enters the membrane there are several chitinous spicules, and to these are attached delicate muscle fibres, which arise from a pair of prominent flanges at the posterior end of the ventral surface of the buccal cavity. According to Nuttall and Shipley the function of this structure is to pump the saliva from the thorax. The contraction of the muscles produces a negative pressure in the receptacle, the elastic rebound of the membrane forcing the saliva outwards.

The pharynx of the mosquito is mainly posterior to the brain, and is

PLATE VII

Figure 1. The head and mouth parts of *Culex fatigans*, in side view. × 43

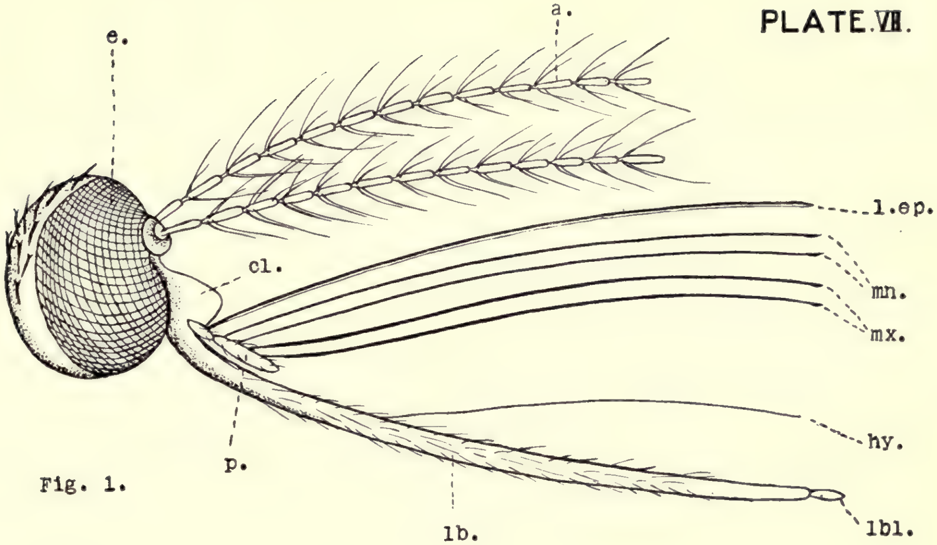
Figure 2. The distal end of the maxilla of same. Very highly magnified.

Figure 3. The distal end of the mandible of same. Very highly magnified.

Figure 4. A cross section of the labium of same, showing the mouth parts in the resting position. l.g., the labial gutter, connected to the mentum by the membrane, mb. ha., haematocoelic space, always exaggerated in sections on account of the shrinkage of the parts. The space is in continuity with the haematocoele of the head and body. hy.c., hypodermal cells. mu., the longitudinal muscle of the labium, which functions in retracting it when the piercing stylets enter the wound. The labium is bent very much as a bow is bent when the bowstring is tightened. × 1000.

Figure 5. The mandible and maxilla of same dissected out in a cleared preparation. The mandible is separated from its attachment. × 170.

PLATE VII.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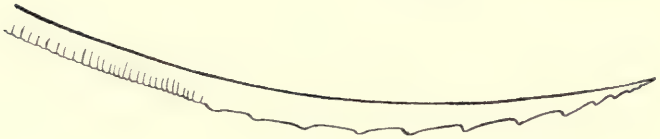

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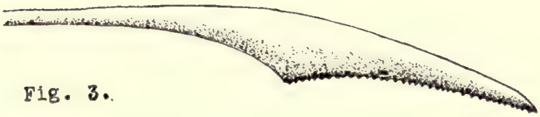
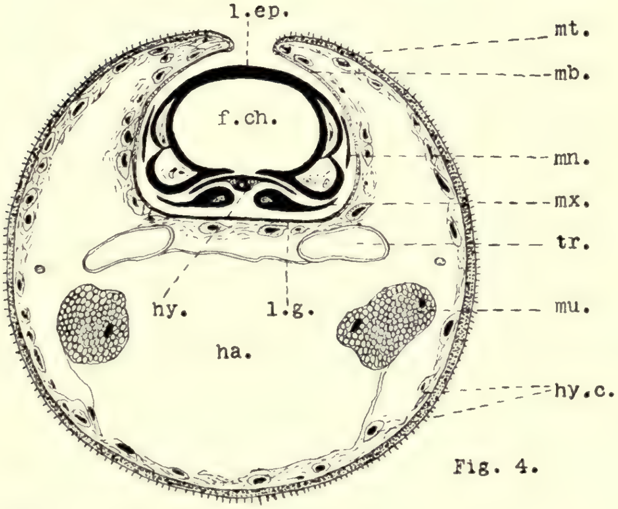


Fig. 3.


l.ep.
mt.
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f.ch.
mn.
mx.
tr.
hy.
l.g.
mu.
ha.
hy.c.

Fig. 4.

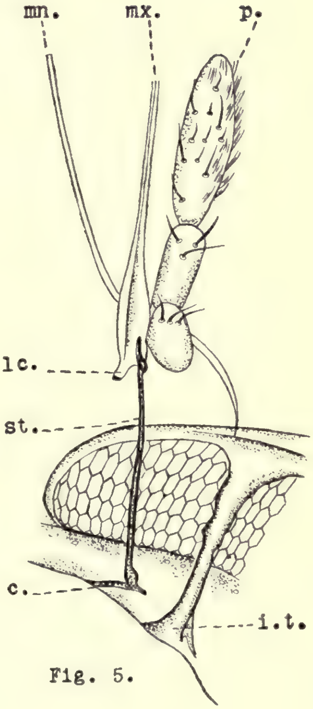

mn.
mx.
p.
lc.
st.
c.
i.t.

Fig. 5.

separated from the buccal cavity by a considerable distance, the interval being bridged over by a chitinous tube, which merges at the two ends with the sucking chambers. This tube is arched with its concavity downwards, the amount of curvature depending upon the angle at which the proboscis is held. In the Anopheline mosquitoes it is only slightly curved, while in *Culex*, in which the buccal cavity and the pharynx are inclined to one another at a considerable angle, the curvature is very marked. The pharynx, when seen from the side, is a pear-shaped organ, continuous by its narrow end with the above tube. It is composed of three chitinous plates, two lateral and one dorsal, attached to one another by membraneous intersections. Each plate is curved in cross-section, with the convexity directed inwards, and in the resting condition the three are in contact with one another, so that the lumen is triradiate. To each of the plates a strong dilator muscle is attached (Plate V, fig. 2), those of the lateral plates arising from the sides of the head cavity behind the eyes, and those of the dorsal plate from the epicranium in the region of the vertex. When the muscles contract the plates are pulled apart, and the lumen made more or less circular.

At the point where the buccal cavity ends and the tube which connects it with the pharynx begins there is, in *Anopheles*, a distinct angle, and at this point there are on the internal aspect of the ventral plate a number of stout hairs of peculiar form, described in detail by Annett, Dutton, and Elliot in *Anopheles costalis*. It is stated that these structures, aided by the angling of the tube, function as a valve.

At the posterior end of the pharynx the chitinous plates are marked by numerous longitudinal ridges, which project on the internal surface as small tubercles. These are adorned with clusters of fine hairs, which, according to Nuttall and Shipley, act as strainers in separating the coarse particles from the food. Where the pharynx is narrowed to become continuous with the oesophagus there is a well developed sphincter muscle.

It will be noted that the buccal cavity in the mosquito is so much smaller than the pharynx that it cannot possibly draw up enough blood to fill the later, and that there is no sphincter muscle between them. Probably the chambers dilate together, communication with the alimentary tract being shut off by the sphincter muscle posterior to the pharynx.

Mechanism of the Biting Apparatus

The reader may remark, in the foregoing account of the mouth parts of the Orthorrapha, and especially with regard to the mosquito, that the account of the mechanism is somewhat different to that usually put forth. The motive force by which the puncture is made is usually ascribed, somewhat vaguely, to the forward thrust of the body. To put this in more precise terms would be to assert that the muscles of the legs thrust the body forward, and that this force is conveyed to the piercing stylets through the neck. There are two reasons why this cannot occur. In the first place, the neck is anatomically incapable of conveying such a thrusting force, being in most cases almost entirely membraneous; and even if it could do so, the force would have to act through an angle which is often nearly a right angle, for the proboscis is not directed in line with the body in the position of action, but perpendicular to it. Even the *Anopheles* mosquito bends its proboscis downwards when it is in use, thus losing any advantage its forwardly directed proboscis might be thought to have. The making of the wound is therefore to be regarded as a function of the appendages, acting by their own muscles, exactly as do the appendages of other arthropods. It might, on a first consideration, be difficult to believe that such minute lancets, actuated by what are after all extremely minute muscles, are capable of making a wound sufficiently deep to draw blood, but the mechanical difficulties are less than they seem. In the first place, one has to remember that rapid contraction is a special characteristic of insect muscle; according to Marey, the wing of a fly can make 330 contractions per second. If it is admitted that the muscles of the appendages can contract at anything approaching this rate, it is easy to understand how the stylets enter the skin. There is, moreover, no waste of effort, for a deep wound of narrow bore is all that is required, and the stylets are elongate and narrow, having a short and sharp cutting edge. In the second place, the shape and thinness of the stylets does not render them as liable to fracture as one might suppose, for they possess a certain amount of flexibility, probably sufficient to enable them to bend if they meet with any resistant tissue when they are thrust in. As the maxillae, which would appear to be the most liable to this sort of injury, cut mainly in retraction, the stress will tend rather to straighten than to bend the blade. Resistance met with during protraction would bend the blade, but no great resistance is likely to be met with at this part of the cutting action, for the majority of the teeth are always directed towards the base of the appendage.

The Prestomum

The labrum-epipharynx and the hypopharynx are commonly included with the mandibles and first maxillae as piercing stylets, and the processes on their distal ends are regarded as teeth. It is most improbable that they take any part in the making of the wound, and it seems certain that the 'teeth' at their distal ends fulfil an entirely different purpose, namely, that of preventing particles too large for its lumen from entering the food canal, a function which would be in keeping with what we know of the nature and origin of these organs. In none of the Orthorraphic biting flies are the processes in the least like the cutting edges or teeth found elsewhere in the Diptera. They are, on the other hand, with the single exception of the hook on the labrum-epipharynx of *Simulium*, mere processes of no greater thickness than the margin from which they arise. There are no muscles attached to the bases of these organs which could effectively impart to them an in-and-out thrust, and any lateral or rotatory movement is anatomically impossible. Moreover, both organs fall a little short of the terminations of the appendages. There are, it is true, some muscles, most easily seen in *Tabanus*, which may retract and protract the buccal cavity, but the utmost limit of protraction cannot bring the terminations of the epipharynx and the hypopharynx to the level of the other cutting points, and indeed it seems more likely that the buccal cavity, and with it these outgrowths, are retracted during the making of the wound, and subsequently thrust down when the level of blood is reached. It should be noted that the only chitinous connection between the labrum-epipharynx and hypopharynx is through the thin slip of chitin by which the labrum is articulated to the clypeus, a condition of affairs which renders it most unlikely that these organs can make any effective thrust.

When the food channel of either *Simulium*, *Ceratopogon*, or *Phlebotomus* is examined from the side with the parts *in sitû*, it is found that the flattened distal ends of the organs are separated from one another by a small interval. The processes on the distal margins are directed across this interval, and those of the two organs come in contact. The opening at the prestomum is therefore guarded by an arrangement which resembles, and presumably acts as, a sieve, preventing the ingress of large particles. The size of the aperture can be regulated by the contractions of the muscle at the base of the labrum.

In *Tabanus* the mechanism appears to be somewhat different. The distal end of the labrum-epipharynx is much broader and stronger than that of the hypopharynx, and in the normal condition of the parts the hypopharynx falls a little short of the termination of the former. The dorsal boundary of the prestomum is thus strong and rigid, while the ventral one is comparatively soft. When the ends of the organs are in a layer of blood, therefore, the latter must enter the canal from a direction posterior to the prestomum; it cannot enter from the front without passing through the tubercles at the tip of the epipharynx, for these are considerably distal to the prestomum, and would in any case separate out any coarse particles. Now when there is a negative pressure in the food canal the soft tip of the hypopharynx will be drawn towards the epipharynx, and the size of the opening diminished, while on the other hand it can be increased by the withdrawal of the labrum by means of the muscle at its base. There is thus a balance maintained between the size of the opening on the one hand and the pressure in the canal on the other, and should any large particle impinge on the end of the food channel it can be at once excluded by the valve-like action of the tip of the hypopharynx.

In the mosquito the mechanism is similar. Here again the tip of the hypopharynx is soft (this is readily seen if *fresh* preparations are examined under a high power) and falls a little short of the tip of the epipharynx. Both organs are flattened at the tip, so that although the food channel between them is circular, the prestomum is a transverse slit, which can be closed by the pressure of the soft end of the hypopharynx against the more rigid epipharynx.

The structures in the buccal cavity and in the pharynx which have been described as sieves are of very doubtful function. It is difficult to see how the fly could get rid of a large particle which had once got so far; the only conceivable method would be a reversed peristalsis, which is most unlikely to occur.

Some such filtering mechanism as this would seem to be a necessity for the fly, when one considers that the wound is made partly by the rasp-like blades on the maxillae, which tear through the tissues, and are very likely to loosen or dislodge particles of greater diameter than that of the food canal.

The Cyclorraphic Diptera

In the Cyclorraphic Diptera the mouth parts are much more differentiated from the primitive arthropod type than in the forms so far considered. The mandibles and first maxillae are absent, and the whole function of obtaining food is transferred to the second maxillae, which have in consequence undergone profound changes. All that remains of the other appendages is a pair of simple palps. In the non-biting flies the inner surfaces of the labella are modified to form a pad by which fluid can be sucked up from moist surfaces, while in the biting forms, for which a cutting apparatus is necessary, a complex arrangement of teeth is developed in the same situation. The external appearance of the proboscis is further altered as a result of the protrusion of a part of the wall of the head capsule, containing the pharynx, to form a part of the proboscis, using the term in the wider sense.

As the question of the origin of the blood-sucking Muscids has arisen in connection with the phylogeny of the parasites which they and their non-biting allies may harbour it will be well to refer briefly to it here. It will also render the somewhat complex structure and mechanism of the parts more easy to explain, if they are looked at from the comparative point of view.

Origin of the Blood-sucking Muscidae

The relations between the mouth parts of the Orthorraphic flies and those of simpler insects, such as the cockroach, have already been pointed out, and the argument may be taken up at the point reached with *Tabanus*. In this insect not only are the mandibles and first maxillae present and functional, but the labium has assumed a function not found in other flies of the same group. The inner surfaces of the labella are provided with a complex arrangement of grooves, by means of which the fly can and does suck up moisture from surfaces, exactly as does *Musca*. The form may be regarded, in fact, as having arrived at the parting of the ways, so far as its method of feeding is concerned. With such a condition of the mouth parts two courses of evolution suggest themselves. Either the fly may remain a blood-sucker, obtaining its food from a wound made by the mandibles and first maxillae, retaining the pseudotracheal membrane as an accessory structure, or perhaps losing it altogether; or it may come more and more to use its oral lobes, and to depend on them for obtaining the whole of its food, so that in course of time the piercing parts disappear. This is what appears to have occurred in the production of the Muscid type of proboscis, now found in a very large number of genera.

The blood-sucking Muscids present no points in common with the blood-sucking Orthorrapha, but are evidently closely related to the non-blood-sucking Muscidae, as shown by their other characters. It is clear from the study of the minute structure of the proboscis that the assumption of the blood-sucking habit has occurred subsequently to the loss of the mandibles and first maxillae. The essential cutting weapons are new structures, having their origin in the inner walls of the labella, as minute chitinous processes. In *Musca domestica* and its allies they appear to be sufficiently strong to act as scraping teeth, capable of scratching a surface from which a fluid food will exude; in one or two other species known they are perhaps powerful enough to scrape off the dried clot from a raw surface, to enable the fly to get at the serum and blood underneath. In those flies which are now confirmed blood-feeders the teeth have become powerful cutting weapons, and there is a specialization of the joints and muscles of the proboscis in conformity with their increased size. The whole proboscis, in fact, becomes altered in the direction of the production of a piercing stylet. The course of the development of this form of cutting apparatus can be traced with remarkable clearness in the present day forms, as will appear from the subsequent descriptions.

In view of these relations, the structure of the proboscis of *Musca* must be understood before passing on to the blood-sucking Muscids. The domestic species of *Musca* are moreover of sufficient importance to the sanitarian as the possible transmitters of disease to warrant a detailed description of their mouth parts, especially since there is reason to believe that it is mainly through the proboscis, which may be transferred from infected material to the food of man very frequently, that infection is conveyed. At the same time it should be noted that there are many species of *Musca*, which, although they have no biting mouth parts, are confirmed blood-feeders, and are theoretically as capable of transmitting pathogenic parasites as are true biting flies. These will be dealt with in Chapter III. The following description refers specially to *Musca nebulo*, the common bazaar fly of Madras, but the differences between species of like habit are so small that it will apply to most of them.

Musca (Plate VIII fig. 1)

The proboscis of *Musca*, in the position of extension, hangs directly downwards from the lower surface of the head, and is roughly cylindrical and blunt pointed. It consists of three parts, named from above downwards the *rostrum*, *haustellum*, and the *labella*. Of these the two latter correspond to the proboscis and labella of the Orthorraphic flies. The rostrum, on the other hand, is a part of the head cavity, which can be protruded at will; it contains the pharynx and the buccal cavity.

The proboscis is completely retractile, and when not in use is withdrawn; the rostrum, reduced in size by the collapse of the air vessels which it contains, passes back into the head cavity, and the haustellum with its labella is concealed on the inferior surface.

Rostrum

The *rostrum* is shaped like a truncated pyramid, with the narrow end directed downwards. Its wall consists of a tough but flexible membrane, which is attached above to the margins of the epistomal orifice, and is continuous below with the walls of the

REFERENCE LETTERS, PLATES VIII TO XIII.

Lettering used more than once is given here. The remainder will be found in the descriptions of the plates.

a. a.	Anterior arch.
a. mu.	Anterior and median set of muscles.
ap.	Apodeme of the labrum.
axp.	Axial apophysis.
b.	Bulb.
b. c.	Buccal cavity.
cl.	Clypeus.
d.ph.	Dilator muscle of the pharynx.
d. s.	Discal sclerite.
ex. h.	Extensor muscle of the haustellum.
f.	Fork of the mentum.
f. ch.	Food channel, formed by the labrum-epipharynx and the hypopharynx.
fl.	Fulcrum.
fu.	Furca.
hy.	Hypopharynx.
k.	Keel of the labial gutter.
l. ep.	Labrum-epipharynx.
l. gl.	Labial gutter.
l. r.	Lateral rod of the labial gutter.
lb. r.	Labellar rod.
lbl.	Labellum.
mb.	Membrane.
mt.	Mentum.
oes.	Œsophagus.
p.	Palp.
p. b.	Petiolated blade.
p. c.	Posterior cornu of fulcrum.
p. m.	Pseudotracheal membrane.
p. mu.	Posterior and lateral set of muscles.
p. s.	Pseudotrachea.
ph.	Pharynx.
r. h.	Retractor muscle of the haustellum.
r. h. p.	Posterior retractor of the haustellum.
r. r.	Retractor of the rostrum.
rd. h.	Rod-like hairs.
sl. d.	Salivary duct.
sl. v.	Salivary valve.
t.	Prestomal tooth.
t. mu.	Transverse set of muscles.
tr.	Trachea.

PLATE VIII

Figure 1. The proboscis of *Musca nebulo*, diagramatic, in side view.

The part above b.c., and including it, is the rostrum. The haustellum extends from this to d.s. The rostrum is rotated backwards and upwards in retraction, on the fixed point formed by the approximation of a.a. to cl., the part being at the same time drawn up by r.h.p. w.r., the membraneous wall of the rostrum. A portion of the side wall of the fulcrum has been removed to show the position of the dilator muscle of the pharynx. The oral lobe of one side is seen from the inner aspect. c.c., collecting channel. e.w., a part of the external wall of the labellum, cut short.

Figure 2. Two isolated rings from a pseudotracheal channel.

Figure 3. A pseudotracheal ring *in sitû*, showing the bifid end, b., with its attached membrane, and its flattened end, f.

Figure 4. The arrangement of the free ends of the rings at the open side of the pseudotracheal channel. Bifid ends and flattened ends alternate. The last three figures, which are of *Calliphora erythrocephala*, after Graham-Smith.

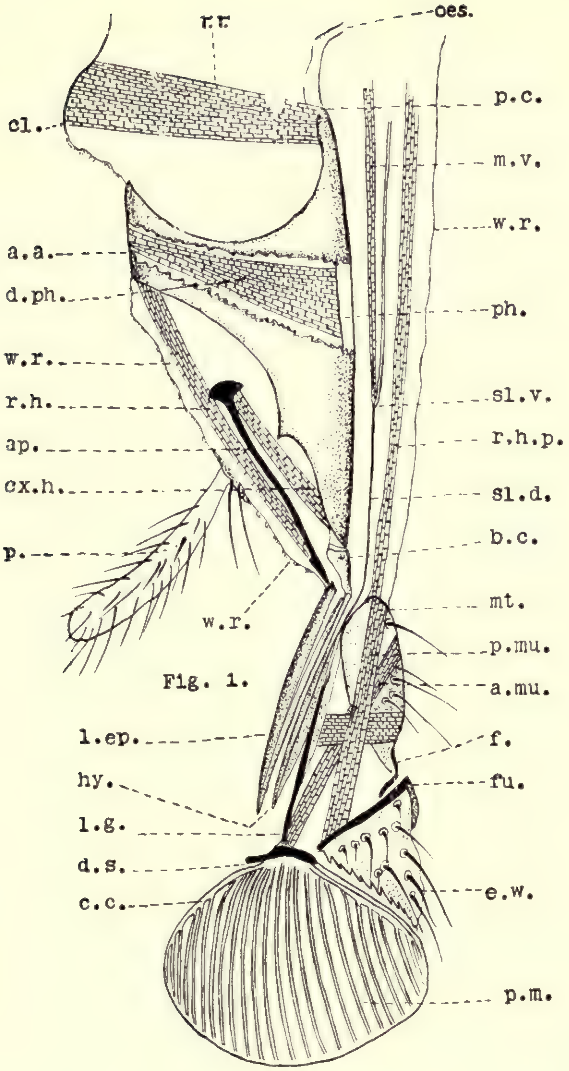
Figure 5. One of the prestomal teeth of *Philaematomyia gurnei*.

Figure 6. The distal end of the labial gutter of *Philaematomyia insignis*, showing the thickened lateral portions which articulate with the discal sclerite. × 150.

Figure 7. The labella of *Lyperosia minuta*, in the position of action. Drawn from a preparation fixed without clearing. The direction in which the teeth and connected structures lie is the reverse of that in the resting position. m.b., the marginal bristles, which in the resting position form a fringe at the distal end of the proboscis. Compare figure 7, Plate XIII.

Figure 8. The teeth and connected structures of *Philaematomyia insignis*. The pseudotracheal channels are not shown. × 500.

PLATE.VIII.


r.r.
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ap.
r.h.p.
cx.h.
sl.d.
p.
b.c.
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Fig. 1.

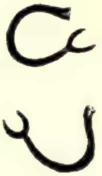


Fig. 2.

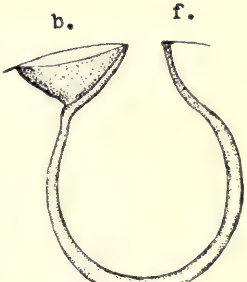
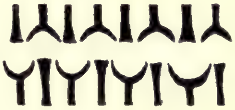


Fig. 3.

Fig. 4.



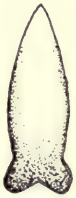
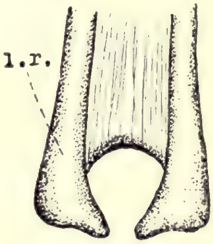


Fig. 5.

Fig. 6.



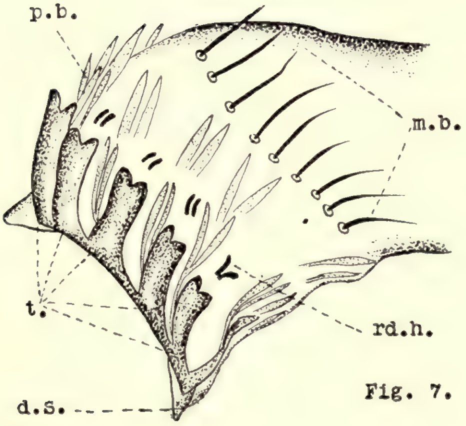

p.b.
m.b.
t.
rd.h.
d.s.

Fig. 7.

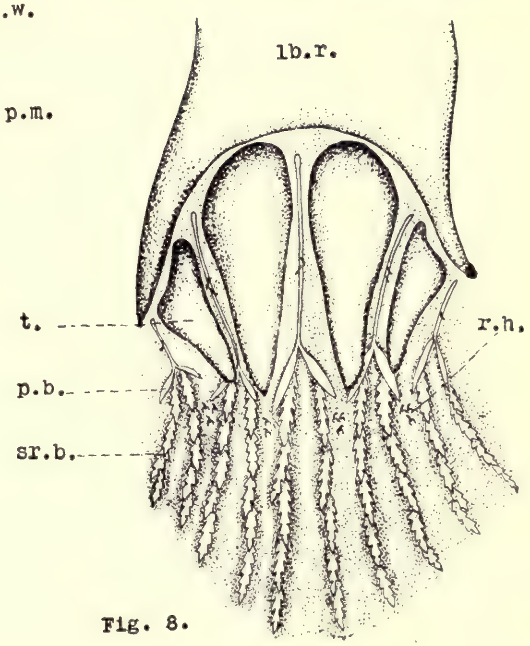

lb.r.
t.
r.h.
p.b.
sr.b.

Fig. 8.

haustellum. The palps, which are composed of a single joint, are attached to its anterior surface; when the proboscis is extended for use they are directed straight forward. Within the rostrum there is a strong chitinous structure known as the *fulcrum*, which contains the pharynx of the fly; this occupies the greater part of the rostrum. The pharynx within it is connected with the food canal in the haustellum by means of a small chamber, the homologue of the buccal cavity in *Tabanus*. In addition to these structures, the rostrum contains certain important muscles and air sacs, and the salivary duct.

The *fulcrum* (Plate VIII, fig. 1), to use Kraepelin's simile, resembles a Spanish stirrup iron ; the foot plate being posterior, and the toe at the lower end. The posterior plate is oblong, concave forwards in both diameters to a slight extent, and produced at the upper end into a pair of conspicuous lateral cornua. At the lower end it is narrowed in the transverse diameter and broadened out a little in the antero-posterior, so that it appears somewhat funnel-shaped. The lateral plates, corresponding to the high sides of the stirrup, are triangular, and are continuous with the sides of the posterior plate. Their free superior and anterior sides are deeply incurved, the curvature on the latter being interrupted by a sharp spine, which projects downward and forward in the lower third. These two lateral sides are connected with one another in front by a transverse arch, which passes between their anterior angles ; this corresponds to the part to which the stirrup leather would be attached. It is roughened and thickened for muscle attachment. The anterior arch of the fulcrum is continuous with the membrane which forms the anterior wall of the rostrum, and can be seen in fresh specimens when the proboscis is extended.

The posterior plate of the fulcrum, as above described, is the ventral wall of the pharynx. Anterior to it there is a thinner plate of a corresponding size, which, in the resting condition, is closely apposed to it, and forms the dorsal wall of the cavity (Plate X, fig. 4). It is traversed down the middle line by a thick and rough ridge, to which most of the dilator muscles are attached. At the upper end the two walls of the pharynx merge to form the oesophagus, while at the lower end they are connected with the walls of the buccal cavity by a short membrane. The space between the lateral walls of the fulcrum is occupied by the dilator muscles of the pharynx, which pass from the anterior arch and the adjacent membrane to the ridge in the middle line of the dorsal wall of the pharynx. When these muscles contract the two plates are drawn apart, and the fluid food is drawn up into the cavity of the pharynx, exactly as in *Tabanus*.

The *buccal cavity* lies partly between the projecting lateral portions of the lower end of the fulcrum. It is a small chamber, formed by a single triangular plate of chitin, the apex of which points downwards, the lateral angles being turned forwards and inwards towards one another and connected by a membrane. Distally the cavity is in communication with the food canal in the proboscis, in a manner which will be described presently. The buccal cavity has no dilator muscles, and plays only a passive part in the mechanism of feeding.

Haustellum

The *haustellum* consists of the labrum-epipharynx, the hypopharynx, and the labium, the latter being divided distally into two labella. Mandibles and first maxillae are absent. The two organs which form the sucking tube are concealed in the groove on the anterior surface of the labium, which alone can be seen without dissection.

The *labrum-epipharynx* (Plate IX, fig. 1), when seen from the front, is shaped like a blunt arrow head. It is a much softer organ than that of *Tabanus*, being composed of much thinner chitin, and having more cellular tissue between the two parts, which are readily distinguished from one another. The labrum gives its shape to the organ, and forms the anterior and lateral sides, and the external thirds of the posterior surface. Where it is deficient in the middle line of the posterior or ventral surface there is a deep chitinous gutter, the epipharynx, connected to the edges of the labrum by a short strip of membrane. The distal end of the organ is flattened and tongue-like, and has on its ventral surface several conspicuous sensory tubercles. Between the two walls there is a series of fan-shaped muscles, arising from the internal surface of the labrum and inserted into the epipharynx.

At the upper end the two parts separate from one another. The labrum becomes continuous with the anterior wall of the rostrum, which is, of course, continuous above with the clypeus. The epipharynx projects a little distance into the rostrum, and is connected with the anterior wall of the buccal cavity by a short membraneous fold.

The labrum is provided with a pair of apodemes, which lie within the rostrum, and are articulated to the labrum at its broad upper end. These are stout sinuous rods of heavily pigmented chitin, pointed at the lower end, and with a short barb-like projection just above the point. Their ends are received into a pair of small pits in the labrum. The upper ends of the apodemes are flattened and broadened, for the insertion of a pair of powerful muscles.

The *hypopharynx* is a soft tongue-shaped organ, rather shorter than the labrum-epipharynx, and is rather broader in its transverse than in its antero-posterior diameter; its lateral borders are produced a little forwards so as to come better into apposition with the epipharynx. Its proximal half is closely fused with the anterior surface of the labium, a feature which is generally found in the non-biting flies, for it is only when the saliva has to be injected into a wound that the hypopharynx becomes free. The salivary duct perforates the whole length of the hypopharynx in the usual manner, as in *Tabanus*. At the upper end the hypopharynx projects into the rostrum posterior to the epipharynx, and is attached in a similar manner to the membraneous wall of the buccal cavity.

The *labium* is roughly cylindrical in shape, broader in the middle than at the two ends, and a little flattened on the anterior surface. Its wall is composed of two plates of chitin, united by a loose membrane. Of these by far the larger is the mentum, an oblong plate, concave on its anterior surface, which forms the posterior and part of the lateral walls. On the anterior surface there is a very thin and narrow plate of chitin, depressed below the rest of the surface, and united in its upper half with the hypopharynx. On either side of this there is a thin but rounded rod of chitin, the two forming the boundaries of the shallow groove in which the labrum-epipharynx and the hypopharynx lie. These rods take an important part in the articulation of the labium with the labella.

Labial Salivary Gland

Within the cavity of the labium there are the intrinsic muscles which move the labella, and the labial salivary gland. The latter is similar to that found in *Tabanus*, and to that of *Philaematomyia*. It is situated at the lower end of the labium, at the point where it divides into the two labella, and consists of a rounded mass of large cells, averaging about forty microns in their long diameter, spherical or oval in shape, and closely compressed together. They lie near the anterior surface of the labium, and have their narrow ends directed towards the surface. The protoplasm is finely granular, and contains usually a single large nucleus, occasionally also an additional small one. At one side of the nucleus there is a permanent vacuole, generally cresentic in outline, and lined by a clear non-staining layer said to consist of chitin. The cells communicate with the exterior by means of fine ducts which arise intracellularly, and unite to form a single channel on each side, opening at the side of the oral pit. The secretion is thus poured out on to the internal or oral surfaces of the labella. Its function is not known.

The Labella

The *labella* are oval lobes, together about the same diameter as the end of the labium when in the position of rest, but capable of great distension and change of form. They are completely separated from one another in front by a fissure which is continuous with the groove on the anterior surface of the labium, and which extends a little distance on to the posterior surface also, partially separating them on that aspect. Each labellum has an outer and an inner wall, which enclose a space continuous with the haematocoele of the labium, and therefore with the rest of the body cavity.

The outer wall is continuous with the outer wall of the labium. It consists of membrane, reinforced, especially at the distal border, with a deposit of chitin sufficient to impart to it a certain amount of rigidity. It bears many long and short hairs scattered over its surface, and a prominent fringe of macrochaetae at the distal margin of the proboscis.

The inner walls of the labella in the resting state are in contact with one another, but when in use are diverged so as to come into the same plane, lying perpendicular to the long axis of the proboscis and in contact with the surface on which the fly is feeding; they are very highly specialized to form the structure known, from the resemblance of its channels to the tracheae or air tubes of the body, as the *pseudotracheal membrane*. This important structure, by means of which the fly absorbs its food, requires a detailed description.

Pseudotracheal Membrane

The groundwork of the inner wall consists of a thin, transparent, and apparently structureless membrane, which is continuous at the distal margin of the proboscis with the outer wall of the labella, and is attached internally to the *discal sclerite*, a ring of chitin which surrounds the prestomum. This membrane is traversed by a number of grooves, which commence at the periphery and converge to the prestomum in a regular manner, the upper ones running inwards and downwards, and the lower ones inwards and upwards. The details of their arrangement differ a good deal in even closely allied species. Usually there are between twenty and thirty grooves altogether, and of these the distal six and the proximal six each unite to form a larger channel, which opens at the prestomum, while the middle channels open directly. Those formed by the union of several separate channels are of a slightly different nature to the rest, and are termed collecting channels.

The minute structure of these channels is very remarkable. Each is an actual depression in the homogenous membrane which forms the inner wall of the labellum. The lumen of the groove, which in section is shaped like a squat flask with a short neck, is kept open by a series of transversely arranged bars of chitin bent to the form of an incomplete loop, the shape of the channel (Plate VIII, figs. 2 and 3). Each of these incomplete rings is bifid at one end and simply expanded at the other; they are set closely side by side throughout the length of the channel, and each ring is placed in the reverse direction to those on either side of it. There is, therefore, a series of alternate bifid ends and expanded ends on each side of the channel (Plate VIII, fig. 4), and over each the membrane is tightly tacked down. When the labella are in use the two ends of each ring are approximated to one another, and there is little if any space between them through which the fluid could pass; the actual openings into the lumen are the shallow grooves between the bifid ends of the rings, at right angles to the long axis of the channel.

Graham-Smith, from whose recent paper many of the above details are taken, terms the space between the arms of the fork the 'interbifid space', and the groove which leads through it to the lumen of the channel the 'interbifid' groove. Now it is evident that, if this be the normal path up which the fluid is sucked, the size of the groove or space will limit the size of the particles which the fly can ingest, a somewhat important point with regard to its disease carrying powers. Graham-Smith gives the following measurements for some parts of the system:—

	PSEUDOTRACHEAE DIAMETER AT		INTERBIFID SPACES DIAMETER NEAR THE ENDS OF THE PSEUDOTRACHEAE	
	Proximal end	Distal end	Proximal	Distal
Calliphora erythrocephala	·02	·01	·006	·004 mm.
Sarcophaga carnaria	·02	·01	·005	·004 mm.
Lucilia caesar	·02	·01	·006	·004 mm.
Fannia (Homolomyia) canicularis	·016	·008	·006	·004 mm.
Ophyra anthrax	·016	·008	·006	·004 mm.
Musca domestica	·016	·008	·004	·003 mm.

The method by which the pseudotracheal channels terminate at the prestomum differs a good deal in different species. In some the rings become increased in depth, and arranged obliquely instead of perpendicular to the surface, and then split in the middle line, the lateral halves separating and coming to lie one in advance of the other. The terminal portions are larger and longer than the rest, and become attached either to the discal sclerite or to the membrane immediately distal to it. In other cases the rings develop a median prominence, directed proximally, and so appear T-shaped. The most proximal of these modified rings is then attached to the prestomum.

The Prestomal Teeth

At the margin of the prestomum, between the terminations of the pseudotracheae, there is a series of minute tooth-like processes, which, though of little importance in the economy of *Musca*, are of great interest as being the homologues of the powerful biting teeth of the blood-sucking forms. They differ in number and arrangement in closely allied species, but preserve a general similarity. Each tooth is an elongate slip of thin chitin, broader at the distal end than proximally, and with a finely serrated but extremely thin margin. The lateral borders are thickened into rods, which articulate with the edge of the discal sclerite. In *Musca domestica* (Plate IX, fig. 5) there are three such rows of teeth, the lateral borders of those of the two distal rows separating from one another and gaining attachment to the membrane between the terminations of the pseudotracheae, while those of the proximal row articulate with the sclerite. There are usually four to six teeth in each row, at each side.

Articulations of the Labella

The articulation between the labium and the labella is divided into two joints, one anterior and the other posterior. Their importance from our present point of view is that they are the homologues of the joints on which the biting apparatus of the blood-sucking forms acts.

The anterior joint is formed by the articulation of the discal sclerite with the rods which form the anterior boundary of the labial gutter. The discal sclerite of *Musca* is a strong loop of chitin, roughly resembling a racket in shape. The rounded distal portion forms the boundary of the prestomum, and has attached to it the inner walls of the labella, or the pseudotracheal membrane, and the prestomal teeth. The portion corresponding to the handle of the racket consists of two stout rods, of about the same length as the looped portion; these lie in almost the same plane as the loop, and diverge from one another as they pass backwards. The sclerite is attached to the lateral rods of the labial gutter by short tendons which pass between the distal ends of the latter and the posterior surface of the sclerite, at the junction of the looped portion and the parallel rods (Plate IX, fig. 8).

The posterior joint lies between the distal end of the mentum and a horse-shoe shaped arch of chitin termed the *furca* (Plate IX, fig. 4). The distal end of the mentum is somewhat contracted, and has in

PLATE IX

Figure 1. The labrum-epipharynx of *Musca nebulo.*

Figure 2. The prestomal teeth and terminations of pseudotracheal channels of *Musca convexifrons,* Thomson. ch.r., the chitinous strands which surround and support the pseudotracheae at their insertions, and are evidently homologous with the teeth. × 450.

Figure 3. Two of the prestomal teeth of *Musca pattoni*, a species allied to the last, and of like habit. Note the difference in the method of termination of the rings of the pseudotrachea. × 600.

Figure 4. The mentum of *Musca nebulo,* m., showing the two divisions of the fork, f. and f'., separated by the incision, i., and supporting the furca, from the median portion of which there is a projection, this being closely fused, like the rest of the furca, with the external wall of the labella. × 100.

Figure 5. A part of the inner wall of the labella of *Musca domestica,* showing the three rows of teeth, t., t'., and t''., and the terminations of the pseudotracheae. In all species of *Musca* examined only the distal portion of the tooth is free from the membrane. After Kræpelin.

Figure 6. The discal sclerite of *Philaematomyia insignis,* attached to the thickened lateral rods, l.r., which form the margins of the labial gutter. The teeth, as shown in figure 8 on the last plate, are attached by membrane, not by rigid chitin, to the concave distal margin. × 250.

Figure 7. The proboscis of *Philaematomyia gurnei,* photographed from a cleared preparation. The labrum-epipharynx, hypopharynx, and labial gutter are placed in order to the left of the palps. The discal sclerite with the attached teeth is dissected from its attachment to the labial gutter, the labellar wall having been ruptured. Microphotograph by Major Kirkpatrick, I. M. S. ×30.

Figure 8. The anterior wall of the haustellum of *Musca nebulo,* with the discal sclerite attached. The hypopharynx is partially fused with the thin labial gutter. Note the lateral rods, attached to the discal sclerite in front and fused with the membraneous wall behind. The membrane, m., connects the mentum and the labial gutter.

PLATE.IX.

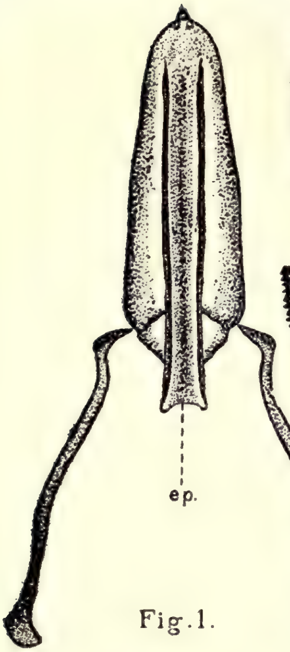


Fig.1.

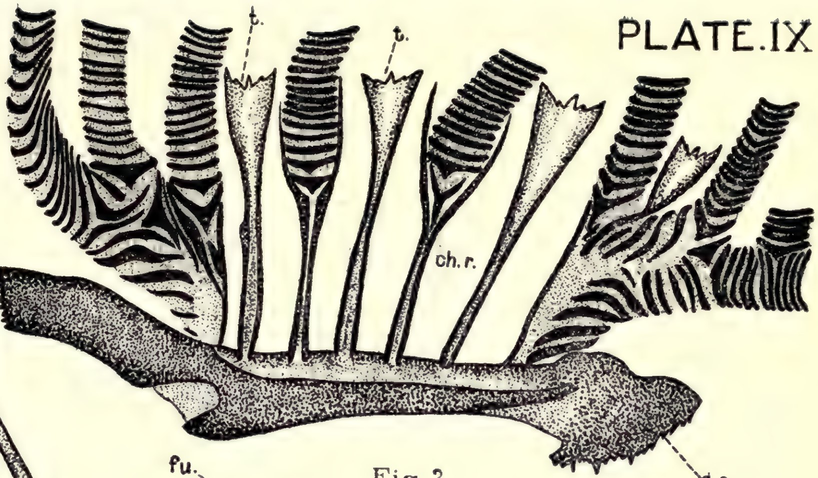


Fig.2.

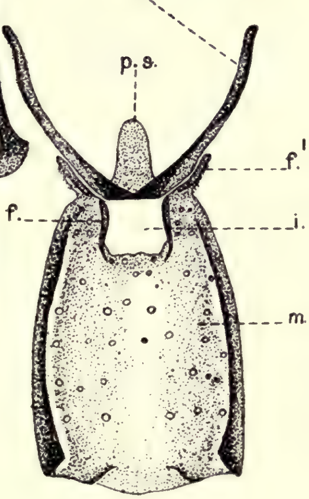


Fig.4.

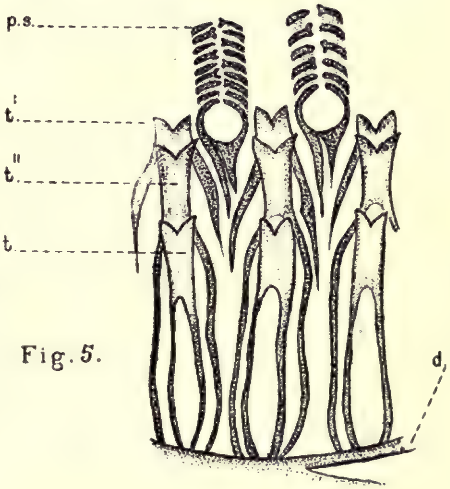


Fig.5.

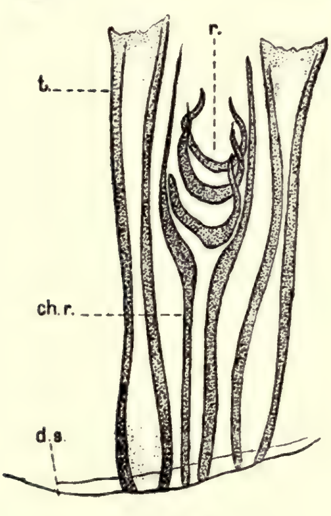


Fig.3.

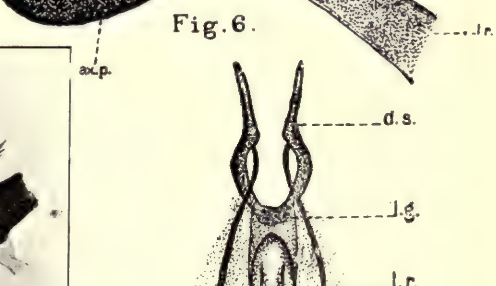


Fig.6.

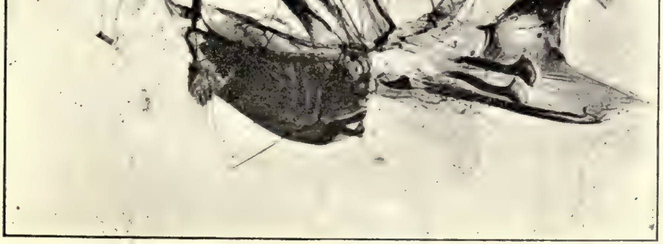


Fig.7.

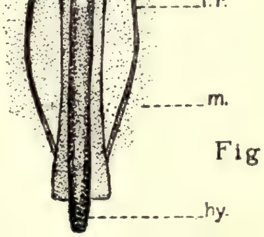


Fig.8.

its margin a square-shaped incision. At each side of this there is a stout chitinous rod, those of the two sides diverging from one another as they pass downwards; the rods have a thinner portion about the middle of their length, so that one may speak of the two halves as the proximal and distal portions of the fork of the mentum. The furca lies between the arms of the fork. It is a thickening of the wall of the labella, and is at every point closely attached to the membraneous wall in this region, so that the labella must always follow it in its movements.

Movements of the Proboscis

The movements of the proboscis are best discussed together with the musculature (Plate VIII, fig. 1), taking each joint in turn. It has already been stated that the proboscis is completely retractile, a fact which will be familiar to all who have watched the movements of the common house fly. The mechanism of extension and retraction will be described first.

Extension of the rostrum on the head is brought about by the rotation of the fulcrum downwards and forwards on the fixed point provided by the attachment of the anterior arch to the epicranial wall. This is brought about, not by direct muscular action, but by the distension of the two large lateral air sacs which are contained within the wall of the rostrum, behind the fulcrum. If one may use the simile, the rostrum is thrust out and straightened as one might extend the finger of a glove by blowing into it. The motive force is provided by the muscles which act in respiration.

Extension of the haustellum on the rostrum is brought about by the contraction of a pair of muscles which arise from the lower end of the fulcrum and are inserted into the expanded upper ends of the labral apodemes. In the resting position the apodemes diverge like the arms of a V, while in the extended position they are almost parallel to one another. As the origin and insertion of the muscles are approximated the labrum-epipharynx, and with it the labium, is straightened on the rostrum; an instance, as Kraepelin remarked, of the application of the parallelogram of forces.

Retraction of the rostrum within the head cavity is brought about by two pairs of muscles, a short pair running between the posterior cornua of the fulcrum and the internal surface of the wall of the head capsule below the antennae, and a long pair passing between the upper end of the mentum and the region of the occipital foramen. The two pairs acting together rotate the fulcrum in a backward and upward direction, and at the same time pull it within the head.

Retraction of the haustellum, or rather flexion of it on the rostrum, is accomplished mainly by a pair of muscles which pass between the anterior arch and the distal ends of the labral apodemes, and act in opposition to the extensors of the haustellum.

In addition to these main muscle bundles there are many more, on both the anterior and posterior sides of the fulcrum, the functions of which are difficult to determine on account of their small size. Their distribution and attachments are described in Kraepelin's paper on *Musca domestica,* and in Hansen's account of *Stomoxys.*

In the labium there are three pairs of muscles, two of which act upon the joints between it and the labella. (Plate VIII, fig. 1, and Plate X, fig. 2.) The first of these is situated in front of and between the other pair, and runs from the upper end of the mentum, and from the posterior surface of the upper end of the labial gutter, to the posterior rods of the discal sclerite. The second, situated behind and rather external to these, is inserted into the lateral arms of the furca. These two pairs of muscles, which are not very clearly differentiated from one another in sections, have a double function. When they contract together the result is that the external wall of the labella is rendered taut, and, through their continuity, the internal wall also; further contraction would result in withdrawing the pseudotracheal membrane and exposing the prestomal teeth. When the anterior muscles alone contract, the discal sclerite is rotated until it becomes perpendicular to the labium. When the posterior pair contracts the external wall of the labella is withdrawn, and the pseudotracheal membrane exposed. Owing to the lax nature of the wall of the labium, contraction of both muscles will also reduce its long diameter and increase its transverse one.

The third muscle is transverse in direction, and runs between the labial gutter and the mentum in the lower part of the labium. It will, therefore, counteract the last mentioned action of the two longitudinal muscles.

Movements of the Labella

The movements of the labella are somewhat complex. In the resting position the space between the two walls is practically nonexistent; the pseudotracheal membranes of the two sides are in contact with one another, and the free ends of the discal sclerite are directed forwards, the labella lying slightly behind the end of the haustellum, while the latter is folded against the retracted rostrum. When they are in use, however, the space between the inner and outer walls of each labellum is distended with the blood of the insect, forced down from the haustellum and the rostrum by respiratory movements, aided probably by the transverse muscle at the lower end of the labium. The discal sclerite is rotated by the anterior set of muscles until the prestomum which it surrounds is parallel with the food surface. The furca is pulled upwards by the posterior muscles, and, as the external walls are pulled out of the way, the internal walls are pulled apart and into a plane perpendicular to that which they occupy in the resting position, until they are parallel with the food surface. When in this position the oral surface of the labella forms a pad, which, by virtue of its fluid contents, is easily applied to even an irregular surface. The fluid can then be sucked through the interbifid grooves and up the food canal, by the muscles of the pharynx.

That the oral lobes are really distended with blood can be easily demonstrated by laying an etherized fly on a slide, and compressing the head gently, without using sufficient force to rupture the contents. First, owing to the pressure driving the air out of the air sacs in the head into those in the rostrum, the latter is extended. Then, on continuing the pressure, the oral lobes are distended, and the pseudotracheal membrane exposed. Sometimes a small trachea ruptures in the manœuvre, and a minute air bubble can be seen to float to the uppermost surface. If the pseudotracheal membrane is punctured with a fine needle while it is distended a drop of a rather viscid yellowish fluid exudes. This is the blood of the fly.

The Blood-sucking Muscidae

The key to the structure and mechanism of the proboscis in the blood-sucking Muscidae lies in the recognition of the homology of the parts with those of the non-biting forms, such as *Musca*. The cutting organs by which the wound is made are the teeth, which are highly elaborated forms of the prestomal teeth as seen in *Musca*.

Before going into the details of structure it will be of advantage to discuss for a moment the directions in which change is to be looked for in the adaptation of the Muscid proboscis to the blood-sucking habit. The first essential is a cutting apparatus, and it is found, therefore, that the teeth become increased in size and strength even in the earliest stages of the evolution. This necessitates increased strength in the structures which support them, and in the muscles and joints through which they come into play. Both the anterior and posterior joints therefore become consolidated, and the discal sclerite undergoes early and marked changes. In the second place, a long and narrow proboscis, terminating in a point, is essential if it is actually to pierce the skin, and in the higher forms the labella are, therefore, reduced in size, the pseudotracheal membrane, no longer required for the absorption of food, disappears, and the labium becomes narrowed in its distal part. The muscles, more powerful than those of *Musca*, are displaced backwards, and are contained in a dilated portion of the labium known as the *bulb*. To ensure rigidity the labium, which now becomes a piercing stylet, is greatly consolidated, the mentum extends further around the surface, and the labial gutter becomes very much thicker. In the higher forms the posterior joint, by means of which the external labellar wall is drawn backwards and the teeth everted, becomes a very important part of the apparatus. At the same time the joints between the haustellum and the rostrum, and between the latter and the head, remain little altered, and although on account of its increased length the haustellum can no longer be concealed when it is retracted, it is held in the same position as that of *Musca*, both in use and in repose. In the higher forms the tip of the haustellum projects conspicuously in front of the head when at rest.

The Genus Philaematomyia

The three species of the genus *Philaematomyia* at present known show separate and early stages of specialization. In all the outward form of the proboscis, as well as that of the fly, is identical with that of *Musca*, except in minor points only found by a careful comparison. The proboscis is completely retractile, and possesses a complete and presumably functional pseudotracheal membrane.

In *Philaematomyia lineata*, Brunetti, the teeth are easily recognized as the homologues of the prestomal teeth of *Musca*. There are four on each side, each shaped like a rose thorn, attached to the membrane between the terminations of the pseudotracheae by expanded bases, and to the edge of the discal sclerite by their rather elongated distal ends. Like those in *Musca*, they show evidence of being composed of two lateral portions. The pseudotracheal membrane shows no change except in the smaller number of channels. The discal sclerite is broadened out distally, so that it becomes more V-shaped, and is much stronger. The hypopharynx, which closely resembles that of *Musca*, is separated completely from the labial gutter, a condition always found in true bloodsucking flies.

The most important advance in structure in this fly is the separation of the discal sclerite (Plate XII, fig. 2) into two parts, a condition which is found to a much more marked degree in all the other more specialized forms. In *lineata* all that can be seen is an oblique fissure running from the internal border of the looped portion of the sclerite, at the junction of the distal and middle thirds, to the posterior end. The sclerite is thus separated into a distal part, which may at once be termed the ***axial apophysis***, including the apex of the sclerite and a small portion of each lateral side; and a proximal portion, including that part which bears the teeth and the rods to which the muscles are attached. The posterior elongated portions may be termed the ***labellar rods***, and the raised flange which bears the teeth the *tooth plate*. The importance of these distinctions will be seen presently.

The next species, ***Philaematomyia gurnei***, Patton and Cragg, (Plate IX, fig. 7) has six well developed teeth and two smaller ones on each side. Each tooth (Plate VIII, fig. 5) has the same general shape as those of the last species, but is thicker, more deeply pigmented, shorter, and has a more expanded base. The bases of the teeth are not united directly to the discal sclerite, but are attached to the membrane by their bases. They are pressed more closely together, their proximal limits forming a curved line which corresponds to that of the tooth plate; the teeth on each side, in fact, fit into the cup-shaped depression in the side of the sclerite.

The discal sclerite is a thick and heavily pigmented structure, in which two parts are clearly differentiated; the axial apophysis is a stout conical piece, the distal end of which is free; the labellar rods are very strong, and are wedge-shaped, the broad ends of the wedges being directed distally, and attached by their internal borders to the axial apophysis. The apophysis thus comes to lie between the two labellar rods, its distal point being on about the same level as the termination of the tooth plate.

The labial gutter in this fly is a thick and densely pigmented structure, which must materially assist in keeping the proboscis rigid under strain. Its articulation with the sclerite, which is placed in a position exactly corresponding with that of *Musca*, is much more defined. On the upper two-thirds of the posterior surface of the gutter there is a median backward projection, extending into the cavity of the labium and dividing the latter into two halves. This is the 'keel' of the labial gutter, and is developed mainly to provide attachment for the muscles which act upon the anterior joint.

The method of termination of the pseudotracheal channels in this species should be particularly noted, for it furnishes the explanation of much more complex structures in the higher forms. The rings become elongated near the border of the sclerite, and divide in the middle line, the parts being of unequal length and placed one in advance of the other. As the sclerite is approached, the segments become longer and more separated from one another, and are also broadened out. The last pair, which are situated opposite one another, are enlarged into broad leaf-like blades, set one on each side of the termination of the channel.

Philaematomyia insignis

Philaematomyia insignis, Austen (Plate X, fig. 1), represents a much more advanced condition, although the outward form of the proboscis remains practically the same. There are four teeth on each side (Plate VIII, fig. 8), of the same shape as those of *gurnei*, but larger and stouter, and more closely approximated at their bases. The two middle teeth are rather larger than the lateral ones, but on account of the curvature of the recess into which they fit the apices of all are on the same level.

Between the teeth there is a well-developed and complex *interdental armature*. This consists of two sets of processes between each two adjacent teeth. Each set consists of five or six small leaf-like blades with deeply serrated edges, arising from a common stalk at different levels and partly superimposed upon one another. The two sets of each pair diverge distally so as to enclose the termination of one of the pseudotracheal channels.

The discal sclerite (Plate IX, fig. 6) in this species is very much modified from that of *Musca*, and one would hardly be able to recognize in them the same structure were it not for the intermediate forms. The two parts are quite distinct. The labellar rods are stout pigmented bars of chitin, flattened from side to side, and almost parallel to one another, but diverging a little posteriorly. About the middle point of each there is a prominent tubercle on the ventral surface; the tubercles of the two sides articulate with the end of the labial gutter, which is moulded to fit them. At the distal end the rods are dilated to form shallow receptacles, in which the bases of the teeth rest (Plate VIII, fig. 8). The axial apophysis is a thick shield-shaped piece of chitin, situated between and behind the labellar rods, binding them firmly together.

The other structures are correspondingly increased in strength. The labial gutter (Plate X, figs. 1 and 2) is thicker than in the last species, and its articulation with the discal sclerite is more definite. The posterior joint, between the fork of the mentum and the furca, is stronger, and the furca itself thicker and rounder than in *Musca*.

The mechanism of the proboscis in these flies appears to be as follows. The rostrum and the haustellum are extended exactly as in *Musca*. The labella are erected by the contraction of the anterior set of muscles attached to the proximal ends of the labellar rods, until, in the case at

PLATE X

Figure 1. The proboscis of *Philaematomyia insignis*, drawn from a cleared preparation. Compare with figure 1, Plate VIII, noting the increase in proportionate length of the haustellum, and the increase in the area of its wall which is chitinized. The simile mentioned on page 39 is realized by imagining that the foot is inserted from left to right between the two posterior cornua, p.c. × 66.

Figure 2. A section through the lower part of the haustellum of *Philaematomyia insignis*. ha., haematocoelic space. The tracheae, not shown in the drawing, are very small at this level. l.sl.g., labial salivary gland, similar to that of *Musca*. × 650.

Figure 3. A section through the lower end of the proboscis of *Lyperosia minuta*. × 755.

Figure 4. A section through the rostrum of *Philaematomyia insignis*, showing the pharynx and its muscles. The tracheal sacs are contracted as a result of shrinkage in fixation. a.w., the anterior wall of the rostrum, here composed of membrane. The section is below the level of the anterior arch of the fulcrum, to which this membrane is attached. × 650.

PLATE X

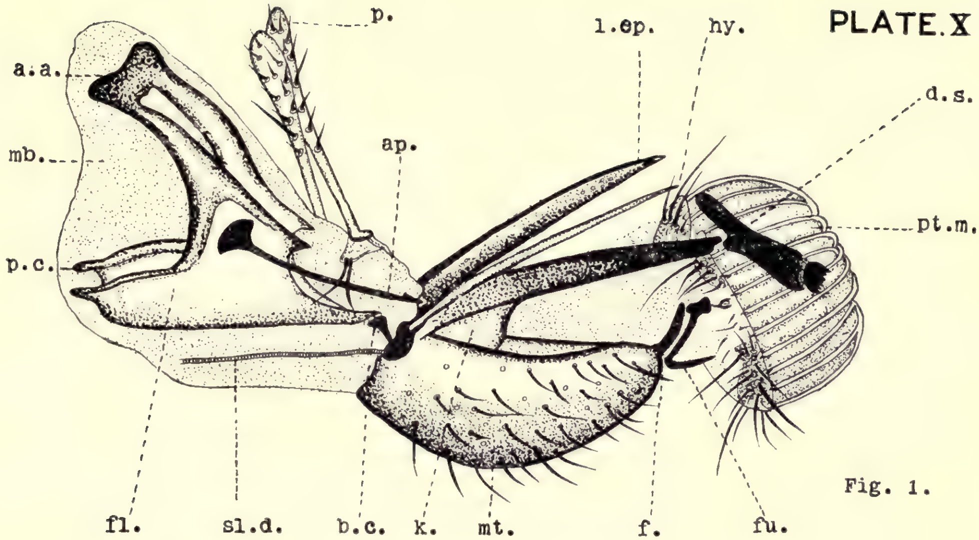

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Fig. 1.

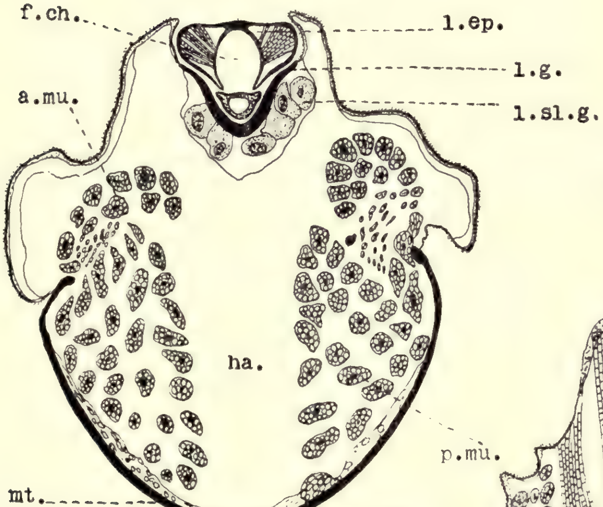
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Fig. 2.

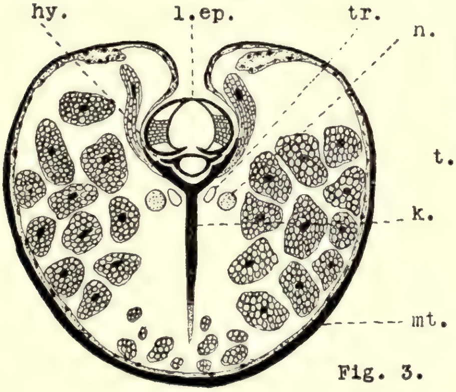
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Fig. 3.

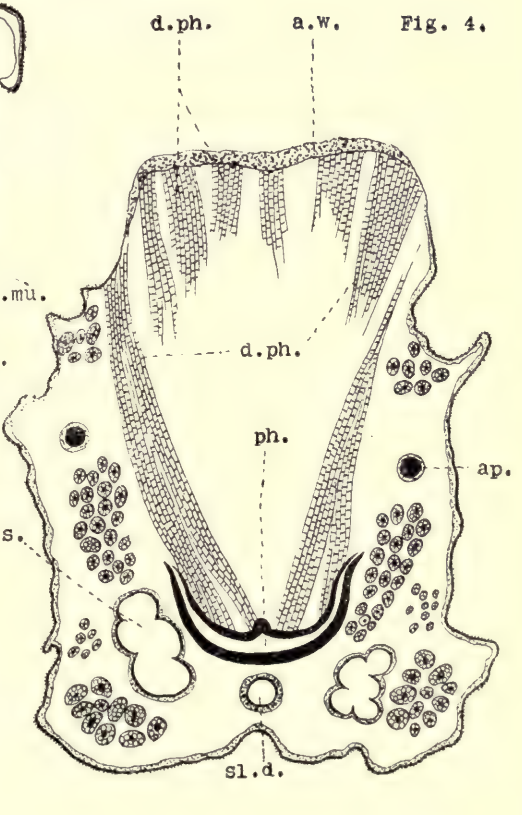
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Fig. 4.

least of *insignis*, the rods are almost in line with the labial gutter. The posterior set of muscles then contracts, and draws the furca upwards, the latter carrying with it the external wall, and through their continuity the internal wall also, till the teeth are rotated outwards on their bases. This turns their cutting edges outwards, and draws them through the wound, and is the essential feature of the cutting act. It is possible that the teeth are also used in a scraping manner, by alternating contractions and relaxations of the anterior set of muscles, the teeth being held in the everted position by the action of the posterior set. The length of the lever to the end of which the teeth are attached would make this action more effective in *insignis* than in any of the others. Whether the pseudotracheal membrane is used in the same way as that of *Musca* it is difficult to say, but it appears probable. The proboscis in this genus is not a piercing organ, and, although the cutting apparatus is an extremely efficient one, the wound made must be a scarification rather than a puncture. Probably the fly bores its way down to the level of the blood by rapidly repeated eversions of the teeth, and by using the everted teeth as a scraper, the discal sclerite being moved up and down on its articulation with the labial gutter; the blood having been reached, it is sucked up through the pseudotracheal channels exactly as is done by *Musca*.

The first two species described are comparatively rare flies and have no special interest apart from their anatomy. The third is common and widely distributed. It is highly probable that if a systematic examination of the proboscides of muscid flies known to be blood-feeders but having a retractile proboscis were made, many more species would be found.

The Stomoxydinae

In the next group of flies, of which *Stomoxys* is the best known example, there is a definite advance in the adaptation of the proboscis to the blood-sucking habit. The proboscis is a true piercing organ, and is actually inserted into the skin.

The most obvious change, one so marked as to obscure the essential similarity, is the elongation of the haustellum. On account of its increased length it can no longer be concealed when it is retracted, and forms a conspicuous projection in front of the head when the fly is at rest. The rostrum, on the other hand, is reduced in size.

In the rostrum, in addition to the smaller size and more compact nature of the part, there is an important modification of the buccal cavity.

The buccal cavity

This has no resemblance to the buccal cavity of *Musca* or to that of the Orthorraphic flies, but has become altered to form a duct with a wide lumen, connecting the lower end of the pharynx with the food canal in the haustellum. The wall of this duct, which is of uniform calibre throughout, is composed of two layers (Plate XII, fig. 4). The internal one is membraneous in the lower part, and composed of thin chitin in the portion lying between the two sides of the fulcrum, which are produced downwards in a funnel-shaped manner. The outer layer is composed of a series of thick chitinous rings set side by side in the same manner as those of a pseudotracheal channel. The rings are open in front, and much thicker posteriorly than at the sides, approaching one another so closely that when seen from the side they appear as if united in the middle line. Such a channel can be bent without its lumen becoming occluded, and will not collapse when the pressure within it is reduced during the sucking action.* In the resting position the rostrum and haustellum are in the same relation to one another as is the case in *Musca*, and the buccal cavity is acutely flexed (Plate XI, fig. 1).

The labium is almost entirely chitinous, the membrane in its wall being confined to a narrow strip which connects the mentum and the labial gutter (Plate X, fig. 3). The mentum is spindle-shaped, narrow in its distal part and expanded at the upper end into the 'bulb', in which the muscles are contained; it extends throughout the sides as well as the posterior surface, leaving only a narrow interval in front. The degree to which the mentum is narrowed distally and expanded above differs in the different genera, and is a good index of the degree of specialization. The labial gutter is not so conspicuous in these forms as it is in *Philaematomyia*, for its place in supporting the biting apparatus is to a great extent taken by the mentum. It is, however, thick and strong in the lower part of the haustellum, in the region of the anterior joint. The 'keel' is not so well developed, and is restricted to the lower half or third of the gutter, this being due to the fact that the anterior joint does not play such an important part in the mechanism, and that consequently its muscles are not so well developed (Plate X, fig. 3).

The Labella in the Stomoxydinae

The labella are small oval lobes, which, when the proboscis is in the position of rest, are little if at all broader than the end of the labium. Each is composed, as in *Musca*, of an inner and an outer wall enclosing a space which is a part of the haematocoele. The outer wall is continuous with the wall of the haustellum and is composed of membrane, in which there are developed plates of thin chitin, the extent of the chitinization and the distribution of the plates differing in the different genera. At the distal margin, where the two walls are continuous, there is a fringe of more or less conspicuous macrochaetae. The inner wall is of about equal extent, and there is in no case a definite pseudotracheal membrane, though in *Haematobia* and *Bdellolarynx* there are well marked traces of it; it is composed of a strong but homogenous sheet of tissue, attached internally to the discal sclerite, and continuous with the external wall at the distal margin of the proboscis. The two inner walls of the labella are in contact with one another in the position of rest, the fissure between them being continuous with the groove on the anterior surface of the labium, and extending for some distance on the posterior surface.

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*A ringed wall of a similar nature is commonly found in the salivary duct, where it has to resist the action of the salivary pump.

The teeth and the interdental armature (Plate XII, fig. 5) are situated at the proximal limit of the inner surface. The *teeth* are oblong structures of considerable size, three to four times as long as broad, pointed at the distal end, and with in most cases a secondary cutting point, produced by a deep indentation of the margin of one side. They are from four to six in number, and are firmly united to one another by their bases, the whole set uniting together proximally to form a thick ridge of chitin, the proximal outline of which is curved to correspond with the distal margin of the discal sclerite. The teeth are attached to the margin of the sclerite by a strong band of fibrous tissue, which is conspicuous in sections on account of its peculiar staining properties. The *interdental armature* consists of one or more rows of leaf-like blades, arising from slender stalks, which are attached to the membrane of the inner wall between the teeth. The arrangement of the armature differs in the different genera, but all conform to the same general type. In *Stomoxys* there is a pair of sets of blades, each consisting of four to six, between each pair of teeth, the two sets of each pair diverging from one another as in *Philaematomyia*. In *Lyperosia* there are two rows of blades, a proximal and a distal, of which the latter are the larger. The blades are extremely thin, and have a finely granular surface.

In addition to the blades, there are on the inner wall certain special structures which probably have a sensory function. The most conspicuous of these are the 'rod-like hairs' first described by Stephens and Newstead in *Stomoxys*. These are short but stout and heavily pigmented, and are situated opposite the apices of the teeth, usually two to each large tooth. They appear to be grooved on one side, though this may be due to the presence of a central channel.

The articulations between the labium and the labella are strong and well defined. The anterior articulation, between the discal sclerite and the labial gutter, is a close one, and permits of only a very limited range of movement, while the posterior one permits of a wider, though much more defined, excursion than that of *Musca* or *Philaematomyia.*

The *discal sclerite* (Plate XII, fig. 3 and Plate XIII, fig. 7) is completely altered in form from the condition seen in *Musca.* It now forms a collar around the prestomum, articulating with the end of the labial gutter behind, and bearing the teeth at the distal end. The parts representing the labellar rods and the axial apophysis are well distinguished from one another. The labellar rods are flattened plates, parallel with one another, but concave on their opposing surfaces, arranged vertically in the long axis of the proboscis, and narrower at the proximal end than distally. The distal margins are concave, to correspond with the curvature of the ridge formed by the united bases of the teeth, to which they are attached on each side by a strong band of fibrous tissue. The narrow proximal ends are moulded to fit the end of the labial gutter ; the dorsal posterior angle of each is hollowed out to an L-shaped notch, into which the lateral rod of the gutter, produced distally and separated from the median ventral portion, is fitted. The middle portion of the gutter is also produced to a blunt point on the ventral aspect, and this fits between the two plates of the sclerite, the whole producing an articulation which can permit of only a limited amount of movement.

The axial apophysis is a thick rounded mass of chitin, situated between and behind the labellar rods, to which it is closely fused; it thus binds them together and forms the floor of the groove. The dorsal side of the groove is open, and is continuous with the groove on the dorsal surface of the labium.

The posterior joint (Plate XII, fig. 1, and Plate XIII, fig. 7), between the fork of the mentum and the furca, is the one on which the most important muscles of the cutting apparatus act. The parts bear little superficial resemblance to those of *Philaematomyia,* for they are moulded to form a strong and compact joint which is capable of bearing a considerable strain. The distal end of the mentum is cut away obliquely upwards and backwards, so that the posterior surface extends considerably beyond the anterior. On the ventral side there are two thick wedge-shaped rods, the broad ends of which are directed towards the labella ; these are the homologues of the proximal portions of the fork of the mentum. The *furca* is a thick chitinous arch, embracing the posterior and lateral aspects of the labella, and so moulded as to

PLATE XI.

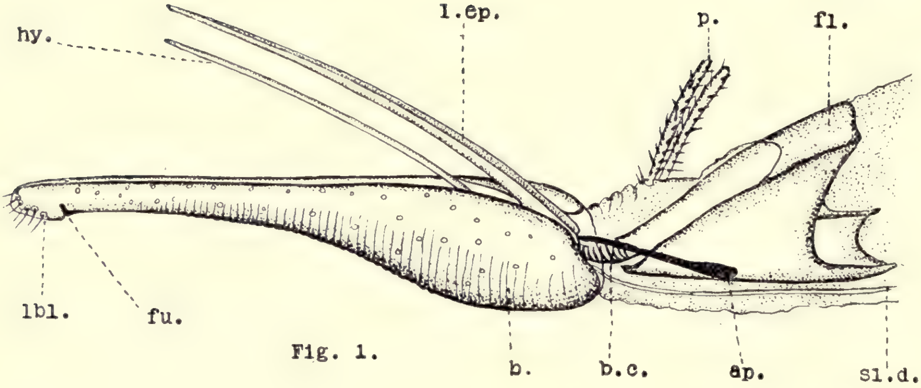
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Fig. 1.

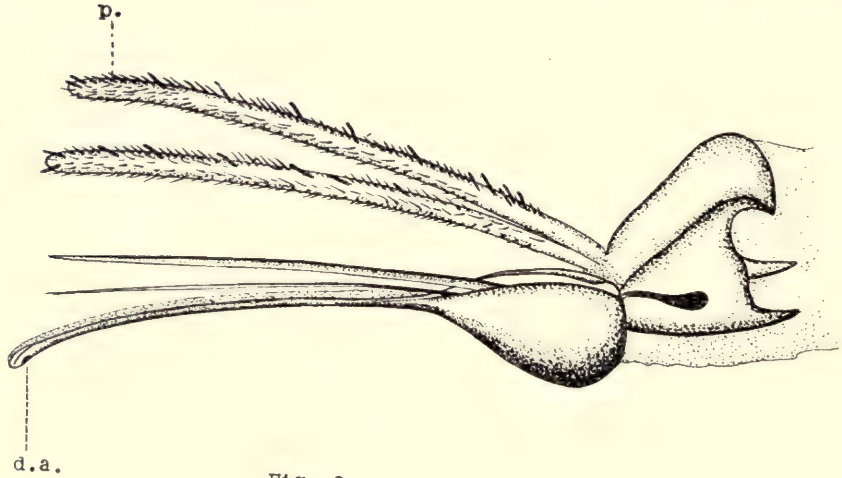

Fig. 2.

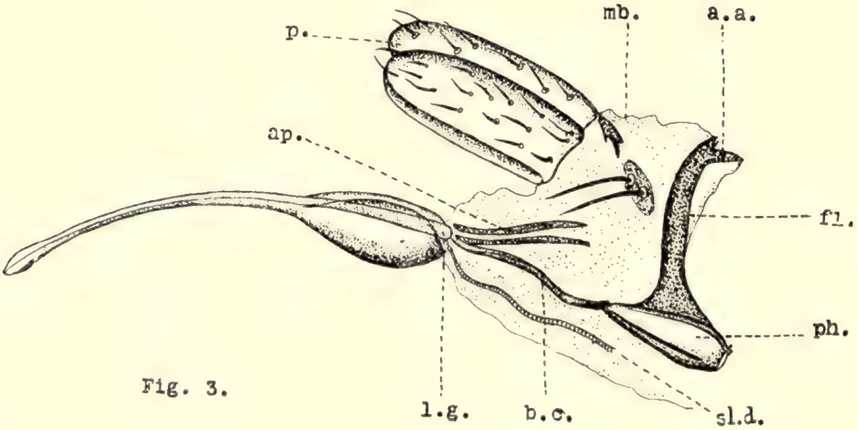
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Fig. 3.

PLATE XI

Figure 1. The proboscis of *Stomoxys calcitrans.* b., the bulb. Note the resemblance of the buccal cavity, which in the Stomoxydinae is merely a tube up which the food is conveyed to the pharynx, to a trachea. In a fresh preparation the tracheae can be seen on either side of it, expanding above into air sacs. × 36.

Figure 2. The proboscis of *Glossina submorsitans.* d.a., the dark area on the posterior surface of the labella, as shown in Plate XIII, figure 8. × 50.

Figure 3. The proboscis of *Hippobosca maculata*, drawn from a cleared preparation dissected out of the head. The parts are shown in the position of full extension. In the resting position the whole of the piercing part of the haustellum is concealed between the palps, while the bulb is within the head. Compare with figure 3, Plate XIII. × 44.

fit closely against the broad ends of the fork. On each side of and behind the furca there is a small rod, closely pressed against the furca but not fused with it, which represents the distal arm of the fork of the mentum, displaced forward and separated from the proximal arm.

It will be noted that there is a triangular space between the lateral arm of the furca and the truncated end of the mentum, when the proboscis is seen in profile (Plate XIII, fig. 7). This is filled in by membrane continuous with the wall of the labellum and with the mentum. In cleared preparations the labial gutter, which is thickest at this point, can be seen at the dorsal side of the triangle. The membrane is strengthened by the presence of numerous small oval plates of chitin, and is thrown into several folds.

Mechanism of the Proboscis

The mechanism of the proboscis in the blood-sucking Muscidae is an extremely interesting one, in view of the close similarity with *Musca*. The rostrum and haustellum are extended and retracted in the manner already described, the only difference being that on account of its increased length the haustellum remains conspicuous in retraction, projecting in front of the head. When extended for use the rostrum and haustellum, as in *Musca*, are brought into line with one another, the proboscis being usually held pointing downwards and a little forwards. The cutting apparatus is then brought into action by the posterior set of muscles, which are attached to the lateral arms of the furca and to the adjacent wall of the labellum. The contraction of these muscles rotates the furca on the fixed point provided by the expanded ends of the mental forks, and as the lateral arms pass backwards they carry with them, because of their close attachments, the external labellar walls. When this occurs the internal walls of the labella are pulled upon, and are carried backwards as far as their attachment to the discal sclerite will permit. As a result of a complete contraction, therefore, the lateral arms of the furca are directed upwards and backwards until they make, with the ventral border of the mentum, a narrow angle open towards the head, the arms themselves lying in the membraneous triangle referred to above; the external wall of the labellum is displaced bodily upwards, retaining its relation to the furca; the internal walls of the labella become external, being rotated through half a circle on their attachment to the discal sclerite, the distal border of which, that is to say, the prestomum, becomes the most distal point of the proboscis. As a result of the eversion of the labellar walls, the teeth and the interdental armature are rotated outwards and upwards on their bases, which are moved with the rest of the internal wall, and as this occurs their cutting points are pulled upwards through the wound, cutting as they go. It is by repeated contractions of these muscles, producing eversion of the teeth, that the wound is made.

In the position of action thus produced (Plate VIII, fig. 7) the interdental armature is swept upwards in advance of the teeth, and as each contraction occurs the blades sweep the surface of the wound clear. When the wound is made, and the fly begins to suck up the blood, they surround the prestomum like a hollow brush, and so prevent the ingress into the canal of particles too large for its lumen, a function of peculiar interest when considered in relation to the homology of the parts, for the interdental armature in the Stomoxydinae is developed from the remains of the rings of the pseudotracheae as seen in *Musca*.

The contractions of the posterior set of muscles are presumably repeated with very great rapidity, as is the case in the biting apparatus of the Orthorraphic flies, and it is necessary to consider by what mechanism the parts can be replaced in position for the next contraction. To understand how this occurs one must revert for a moment to the structure of the labella. In the resting position the prestomum is at some distance from the distal end of the proboscis, being in fact separated from it by the total depth of the inner walls. This may be regarded as an invagination, the distal borders of the sclerite, which bound the prestomum, being the apex. Now when the external wall is displaced upwards and the inner wall everted, this invagination is undone, and the blood which was between its inner and outer walls is driven upwards. The return of the parts to the resting position is brought about by the pressure of blood in the proboscis, in exactly the same way as is the case in the distension of the oral lobes of *Musca*. This is due partly to the respiratory movements of the fly, and partly to the contraction of the transverse muscles which pass between the mentum and the labial gutter, in the lower end of the labium.

The muscles of the labium are divided into the same bundles as in *Musca*. The posterior set, however, which has to pull the teeth through the tissues, and has therefore to act against considerable resistance, is very much larger than the others, and occupies practically the whole of the bulb. In the narrow part of the proboscis the muscle fibres are replaced by tendons, which spread out at their insertions so as to gain attachment to the external wall of the labellum, as well as to the furca. The anterior set, which in *Philaematomyia* erects the labellar rods, is not well developed, for the anterior joint is practically fixed in a position of incomplete extension.

Labrum-epipharynx and hypopharynx

The labrum-epipharynx and the hypopharynx are much more slender and narrower than those of *Musca*, since they are more effectively concealed and protected by the deeper labial gutter. The canal for the food is formed in the same way, but with this notable difference, that in the upper part of the haustellum it becomes closed by the fusion of the sides of the groove formed by the epipharynx, and the union of the dorsal lamina of the hypopharynx with this. The hypopharynx is free from the labial gutter except at the upper end.

Both the labrum-epipharynx and the hypopharynx are shorter than the rest of the haustellum, and do not, in the resting position, reach beyond the level of the furca. They cannot, therefore, take any part in the making of the wound, and have, as one would expect, thin and flaccid distal ends. On the ventral surface of the distal end of the epipharynx there are several sensory tubercles or hairs, which, as they are situated at the opening of the food canal, probably play a part in the mechanism by which the size of the opening is regulated.

The distance between the terminations of the labrum-epipharynx and hypopharynx and the margin of the prestomum, as defined by the discal sclerite, is materially reduced in the position of action, when the wound has been made to a satisfactory depth, by a longitudinal compression of the mentum. The surface of the latter is marked by a series of transverse ridges and furrows, which extend all round the organ, and are the most marked in its narrowest part. The deepening of the furrows must be accompanied by a decrease in the length of the labium. This is brought about by the further contraction of the powerful muscles of the bulb, which press the furca against the fork of the mentum, and so compress the latter towards its proximal end. The ridges and furrows are always more marked in specimens fixed in the everted position than in those in which the labella are closed.

The tracheal structures in the proboscis are the same as those of *Musca* and *Philaematomyia*. One interesting point may be noted with regard to the nerves. There is one large nerve on each side of the cavity of the labium, in close contact with the trachea. At the upper end of the haustellum the trachea is very much the larger of the two, but as they pass downward it diminishes rapidly in size as it gives off branches for the supply of the muscles. The nerve becomes only a little smaller, and as it enters the labellum is larger than the trachea. The labella, while they require comparatively little supply of air, require a rich supply of nerves for their complex mechanism.

The labial salivary gland does not occur in the Stomoxydinae, having disappeared with the pseudotracheal membrane.

It has been stated that in the proboscis of *Haematobia* there are to be found vestiges of a pseudotracheal membrane. In all other respects the mouth parts are similar to those of *Stomoxys*, such differences as there are, as for instance a rather less marked spindle shape in the labium, and a smaller disproportion between the length of the rostrum and haustellum, indicating that the fly is not so far advanced in specialization as the rest of the group. At the distal end of the labella there are five small triangular flaps (Plate XII, fig. 1), each composed of an inner and an outer wall, continuous with the walls of the labella, and enclosing between them a space which is continuous with the haematocoele. The wall consists for the most part of a thin transparent membrane, strengthened by small oval chitinous squamae, and resembles that found elsewhere in the non-chitinized area of the proboscis in other Stomoxydinae. In the middle line of the inner wall, however, these squamae are elongated transversely, and arranged in a row so as to form a shallow gutter; as the region of the teeth is approached they are gradually replaced by definite pseudotracheal rings, similar to those of *Musca*, except that the channels do not appear to be quite so narrow at the neck. Presumably the channels in the flaps and on the inner walls of the labella are used in the same way as those of *Musca*, to suck up the blood, when the haematocoele of the labella is distended. A similar condition is found in *Bdellolarynx*.

Haematobia

The proboscis of *Glossina* (Plate XI, fig. 2) is modified from the *Musca* type in very much the same manner as that of the Stomoxydinae, but the specialization has gone very much further. The homology can, however, be followed fairly closely, and the mechanism is practically the same.

The proboscis is held in front of the head when at rest, but is concealed by the palps, which extend to its tip. On account of the great elongation of the haustellum, which in this genus is at least three and a half times as long as the rostrum, the proboscis is very conspicuous even in the resting position.

Glossina

The rostrum has the shape of a very short pyramid, and is almost entirely occupied by the fulcrum, this being more compact and more

PLATE XII

Figure 1. The labella of *Haematobia stimulans*, drawn from a cleared preparation. fl., the flaps, on the internal surfaces of which are to be found the pseudotracheae. p.b., the position of the petiolated blades. p.s., the position of the pseudotracheae, in the resting condition. m.f., the upper division of the fork of the mentum, on which rests the furca. m., the mentum. × 150.

Figure 2. The discal sclerite of *Philaematomyia lineata*. t.p., the flange which projects from the distal ends of the labellar rods, and to which the teeth are attached. × 470.

Figure 3. The discal sclerite and distal end of the labial gutter of *Stomoxys calcitrans*. m.g., the median portion of the gutter. The commencement of the keel is shown. The teeth are attached by a strong but flexible band of fibres to the concave distal end of the sclerite. ×450.

Figure 4. The lower end of the pharynx of *Haematobia stimulans*, seen from behind, to show the nature of the wall of the buccal cavity. r., the rings of chitin which surround the tube. ×350.

Figure 5. The teeth and connected structures of *Haematobia stimulans*, detached from the discal sclerite. ×525.

Figure 6. An isolated tooth, (*Haematobia stimulans*) to show the secondary teeth on its inner surface. These secondary teeth become external when the teeth are everted.

PLATE. XII.

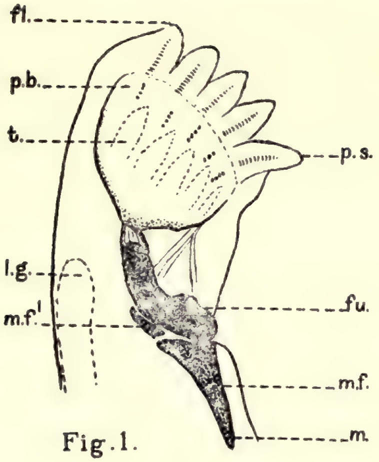
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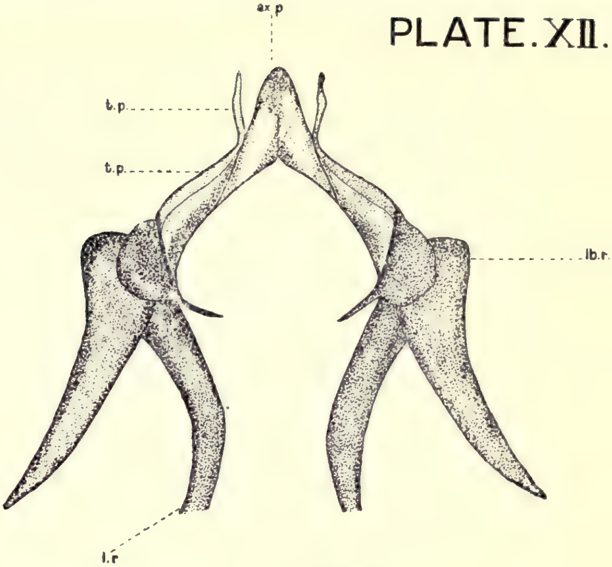
Fig. 1.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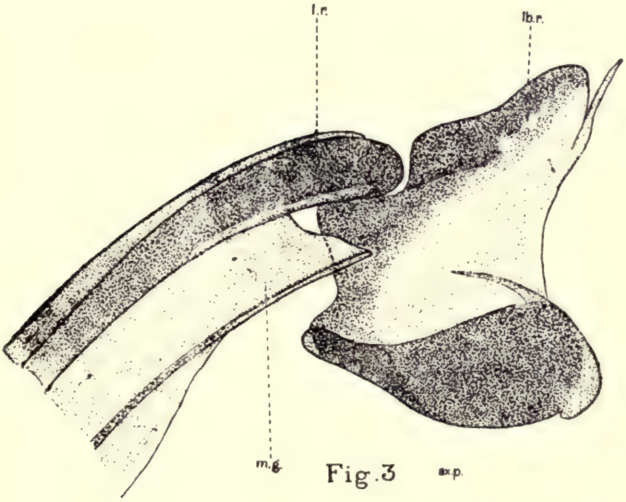
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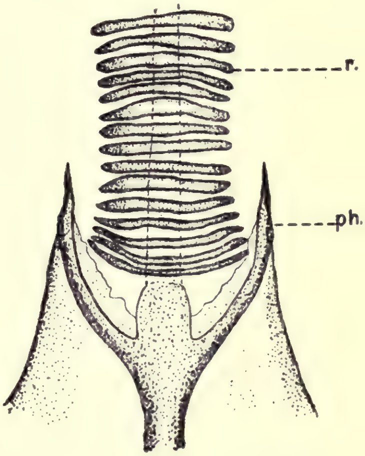
Fig. 3



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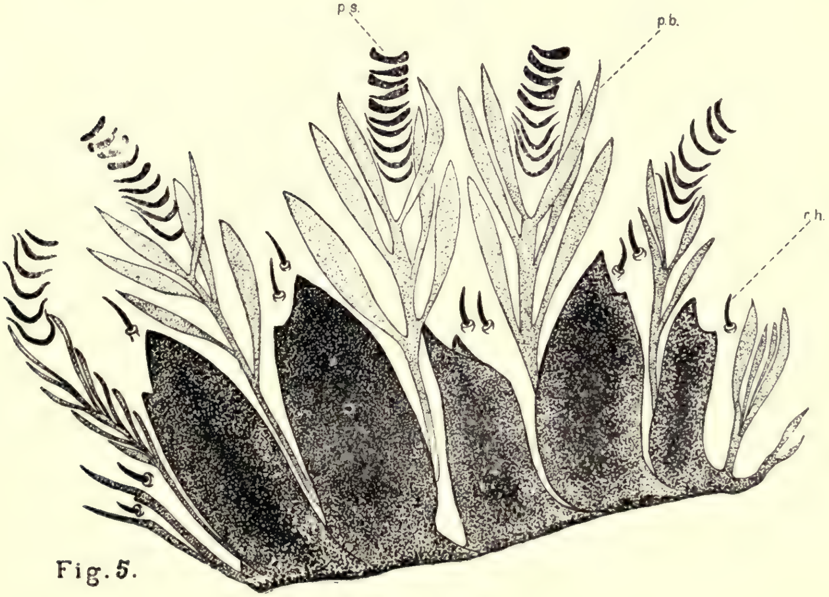


Fig. 5.

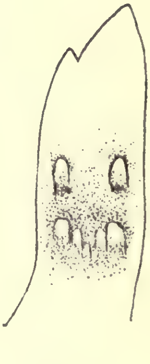


Fig. 3.

evenly chitinized than in the Stomoxydinae. The labral apodemes are correspondingly reduced, and are also thinner than those of the forms so far dealt with. The buccal cavity is of the same type as that of *Musca*, and consists of a small chamber, broader than long, and formed from a single plate of chitin, the lateral edges of which are turned forwards and connected across the front by tough membrane; the epipharynx and hypopharynx terminate at this point in a manner similar to that described for *Musca*.

The haustellum appears on external examination to be an exaggeration of the form seen in *Stomoxys*. It consists of two portions, the upper end being swollen and bulbous, the distal part narrowed down to a fine stylet; the relative proportions of these being approximately one to two and a half. When examined in sections and in cleared preparations it is found that there are many important differences from the proboscis in the Stomoxydinae. In the first place, the labella are not nearly so well marked off from the labium proper, and are only very slightly thicker than the adjacent part of the proboscis; secondly, the labial gutter, and not the mentum, is the main support of the proboscis.

The labrum-epipharynx lies throughout in close contact with the labial gutter, and since it does not, on that account, need to possess much rigidity, it is a very delicate organ. The two constituent parts are closely welded together, with only a small interval between them at the sides, and together form a long inverted gutter; at the distal end, which is situated just distal to the junction of the labium with the labella, the gutter is very shallow, but further up the lateral portions are produced in a circular direction, so that at the upper end the groove is converted to a tunnel with only a small gap in its ventral wall.

The external surfaces are in contact with the labial gutter, and are provided with a row of short teeth which interlock with a corresponding set on the gutter, the arrangement serving to prevent any displacement of the organ from the groove in which it lies. The distal end is flattened and soft, and is provided with a number of fine sensory hairs. At the proximal end the two parts separate in the usual manner, the labrum becoming continuous with the membraneous anterior wall of the rostrum, the epipharynx fusing with the anterior wall of the buccal cavity.

The hypopharynx is an exceedingly delicate organ, composed of thin and semi-membraneous chitin; it does not assume the flattened form seen in the other Diptera, and consists of little more than the wall of the salivary duct, with some lateral membraneous expansions in the region of the bulb. For a considerable part of its extent, according to Stephens and

Newstead, it is actually connected to the lateral extremities of the labrum by a fine membrane, so that the food canal in the haustellum becomes a closed tube. The organ lies for the most part of its length in a small median recess in the labial gutter.

The mentum in the bulb presents no special characters, but in the narrow part of the proboscis the chitin is very thin and semi-membraneous, and bears a number of peculiar spines on the ventral surface, arranged in two parallel rows. It is connected to the labial gutter by a narrow membrane divided into polygonal areas. The labial gutter is composed of thick chitin, and contributes much more to the rigidity of the proboscis than the mentum. In the middle of the haustellum it forms an almost complete tube, rather broader in the transverse diameter than in the vertical, and with a deep and narrow pocket in the middle ventral line for the reception of the hypopharynx. The lateral portions are thinner and pointed, and overlap the labrum, to which they are connected by the row of interlocking teeth mentioned above; at this level the sides of the mentum are also thickened, so that there is very little space left between the anterior and posterior walls of the labium. Distally the walls of the gutter become thinner, and are directly continuous with the inner walls of the labella, no discal sclerite being differentiated in this form. At the upper end of the labium the sides of the gutter are more widely separated from one another, and the labrum appears on the dorsal surface of the proboscis.

Biting apparatus of Glossina

The biting apparatus (Plate XIII, fig. 9) consists of prestomal teeth evidently homologous with those of *Musca*, and in addition the 'rasps', and certain sharp spines on the outer wall of the labellum. The arrangement at the prestomum is as follows. On each of the internal labellar walls there are two fissures, which divide it into three equal portions, dorsal, middle, and ventral. The main part of each division consists of a 'rasp', an oblong plate, longest in the antero-posterior diameter, and traversed by about ten ridges running from the dorsal to the ventral side; each of these is in turn being divided into minute ridges running in the long axis of the proboscis. At the distal end of each rasp there are two large conical teeth, the internal ones of the dorsal and ventral sets being larger than the external. These large teeth arise from a small chitinous eminence, at the sides of which there are two smaller teeth. Between the two larger teeth of each division, and also on the dorsal and ventral surfaces of the inner wall, there is a set of excessively fine scales, arranged in a fan-shaped manner, which represent the interdental armature. These are termed by Stephens and Newstead the ' fans '.

The mechanism of the biting apparatus (Plate XIII, fig. 8), is a modification of that described in the Stomoxydinae. On account of the disappearance of the discal sclerite there is no anterior joint, all the movements taking place on the posterior one. The furca is represented by a broad but rather thin transverse bar, the lateral arms of which turn forwards and upwards on to the sides of the labella, and are there received into shallow pits in the external wall. The fork of the mentum is represented by a thickening of the chitin immediately posterior to the furca, and consists of two lateral rods united by their broad distal ends, and so closely opposed to the furca that they appear to form with it a T-shaped piece. Both the furca and these forks are simple thickenings of the chitin, not nearly so well demarcated as the corresponding parts in *Stomoxys*, and not raised above the surface.

The external walls of the labella are partly membraneous and partly chitinous. On the posterior surface there is a circular area, situated about midway between the distal end and the furca, in which the wall is thickly chitinized and pigmented. This part, referred to by Stephens and Newstead as the 'dark area ', is readily recognized under a low magnification. Posterior to this the wall is membraneous as far as the furca. The lateral walls are mainly chitinized, and are produced at the posterior ends to a sharp angle on each side. Distal to these angles, and considerably removed from them in the position of rest, there is a pair of small pits at the end of longitudinal thickenings on the lateral wall of the mentum.

The muscles of the bulb, which cannot readily be separated into bundles, terminate in long tendons which traverse the whole of the narrow part of the mentum, and are inserted partly into the lateral arms of the furca and partly into the thick and pigmented area anterior to it. When they contract the furca, which is fitted into a groove on the distal end of the fused rods, is rotated in the usual manner, so that its lateral arms come to point in the reverse direction, that is, towards the base of the proboscis. As the tendons are also inserted into the chitinized area distal to the furca, the posterior wall as a whole is drawn upwards together with it, so that there is a complete change in the relations of the parts. The dark area is approximated to the middle portion of the furca, and the posterior angles of the external walls are pulled upwards till they fit into the pits on the lateral wall of the mentum. The teeth and rasps are everted and pulled upwards through the wound in the usual manner, following the movement of the external wall.

The proboscis of *Glossina* is inserted into the skin for a considerable depth, and the eversion of the teeth and upward displacement of the external wall must be repeated with very great rapidity. Several observers have noticed that when the fly commences to feed it produces a faint humming sound, due to a rapid vibration of the wings; this is probably due to the extremely rapid respiratory movements by which the blood is forced down into the labella, in order to reduce them to the resting position in readiness for the next cutting act.

The attitude of the fly while feeding is rather different to that of the Stomoxydinae, for owing to the reduction of the amount of movement possible between the rostrum and the head, and between the rostrum and the haustellum, the fly has to raise itself a little on its hind legs in order to adjust the tip of its proboscis to a position suitable for feeding.

Hippobosca (Plate XI, fig. 3)

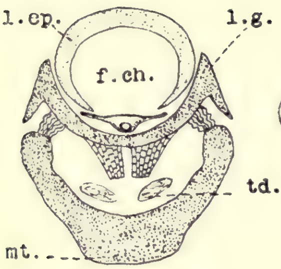
Hippobosca and its allies present a curious condition, for while the upper part of the proboscis, or rather the sucking apparatus simply, as it is never protruded from the head, resembles that of *Musca* in many respects, the distal part or proboscis proper is more like that of *Glossina.* The Pupipara are not descended from a Glossina-like form, but from some remote ancestor common to it and to *Musca.*

In the resting condition the whole of the sucking apparatus, corresponding to the rostrum of *Musca,* and also the posterior part of the haustellum, are concealed within the head. The distal part of the haustellum, which, as in *Glossina,* forms a narrow piercing stylet, is concealed between the palps, which alone are visible without dissection. (Plate XIII, fig. 3.) When the mouth parts are required for use the fulcrum is rotated in the same manner as in *Musca,* and by a similar mechanism, with the result that the stylet is pushed forward between the palps, and the pharynx, buccal cavity, and haustellum brought into line with one another.

The Sucking apparatus of Hippobosca

The fulcrum and pharynx are of the same type as in *Musca,* but differ in detail. The ventral plate is strongly concave, and terminates posteriorly in very small outwardly directed cornua. The lateral plates are narrow, and converge towards one another in a V-shaped manner; the anterior arch is represented only by a short rod of thick chitin which lies between the ends of the lateral plates and is directed antero-posteriorly. (Plate XIII, fig. 6.) It is fitted into a semicircular notch at the distal end of the plate of chitin which separates the eyes. The ventral wall of the pharynx

PLATE. XIII.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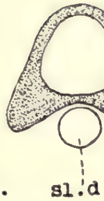

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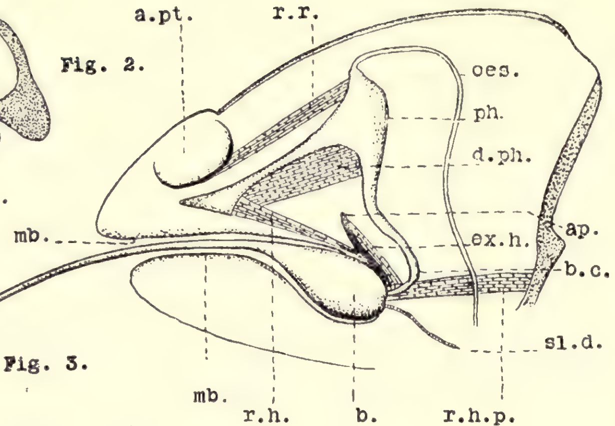
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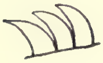

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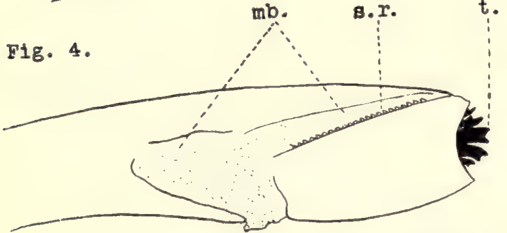

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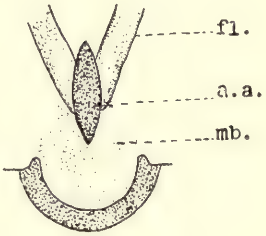

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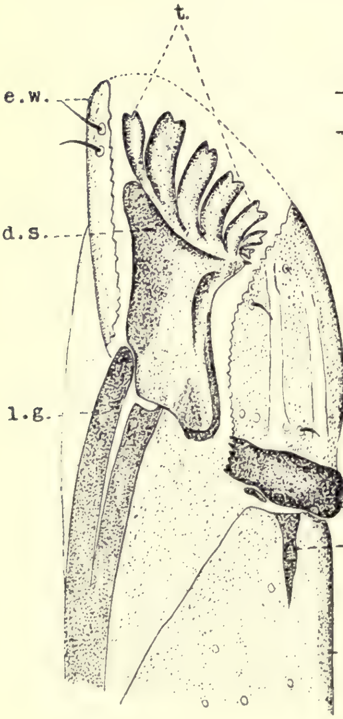
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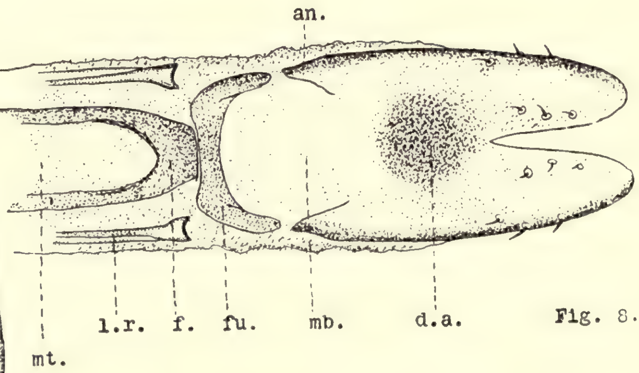
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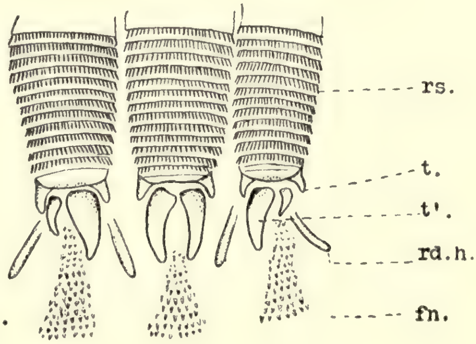

Fig. 9.

PLATE XIII

Figure 1. Cross section of the narrow part of the haustellum of *Hippobosca maculata*. At this level the labrum and epipharynx are completely fused. Higher up the two separate. td., the tendon of the muscle of the bulb, which retracts the labellar wall and everts the teeth. × 450.

Figure 2. A section through the lower part of the buccal cavity. × 400.

Figure 3. The proboscis and sucking apparatus of *Hippobosca maculata* in the position of rest, within the head. The palps, which conceal the projecting part of the haustellum, are not shown. Note the invagination of the membrane around the haustellum, to be attached to the base of the bulb as in *Stomoxys*. a.pt., the antennal pit, sunk below the surface of the head. × 50.

Figure 4. Three of the teeth of the serrated ridge on the outer wall of the labella. s.r. in next figure.

Figure 5. The distal end of the proboscis of *Hippobosca maculata*, showing the membraneous interval which permits of the eversion of the wall. s.r., the serrated ridge bearing the teeth shown in the last figure. × 200.

Figure 6. The articulation of the anterior arch of the fulcrum with the wall of the head between the antennal pits. The distal edge of the wall is notched for the reception of the fulcrum.

Figure 7. The distal end of the proboscis of *Lyperosia minuta*, with a part of the external wall cut away to show the teeth. × 700.

Figure 8. The distal end of the proboscis of *Glossina submorsitans*, seen from the posterior surface. d.a., the dark area. an., prominent angles which fit, in eversion, into the cup-shaped tubercles on l.r., lateral thickenings in the wall of the mentum. × 200.

Figure 9. The structures on the inner wall of the labellum of *Glossina submorsitans*. rs., the rasps. t., t′., the teeth. fn., the 'fans', representing the interdental armature. × 900.

is almost entirely composed of a thick membrane, there being only a small elongate area in the middle line which is strongly chitinized; the main mass of the dilator muscles of the pharynx are inserted into this median area.

The buccal cavity in this form has the shape of a long chitinous tube, which connects the pharynx with the food canal in the haustellum. The lateral walls of the tube are much thicker than the dorsal and ventral walls, and project outwards and backwards in the distal portion of the tube so as to form a shallow groove for the reception of the salivary duct. The lumen of the tube is of uniform diameter throughout, and is circular, though a little narrower in the dorsal than in the ventral half. (Plate XIII, fig. 2.) At the upper end of the buccal cavity its walls are continuous with those of the pharynx, while at the distal end the union with the food canal in the haustellum is brought about in a manner similar to that of *Musca*; the cavity is slightly dilated, and encloses the end of the food canal, which is here a closed tube. The edges are united by a short membrane, so that although the continuity of the tube is maintained, free movement is possible.

The haustellum strongly resembles that of *Glossina*. The bulb occupies only the upper third; the narrow part distal to this is curved downwards and forwards, and terminates in a cutting apparatus much simpler than that of the Muscidae. The end of the labium is not clearly divided into two labella, but the structures which make up the biting apparatus are bilaterally arranged.

The labrum-epipharynx is a relatively strong organ, shaped like a long and narrow arrow-head, and rounded on the dorsal surface. (Plate XIII, fig. 1.) It is not enclosed by the labial gutter, but forms the dorsal aspect of the haustellum, and is beset with two parallel rows of minute spines. The labrum and epipharynx are closely fused together in the distal part of the proboscis, but separate higher up; the distal end of the labrum is fused with a membrane corresponding to the anterior surface of the rostrum, while the epipharynx forms a closed tube by the union of its sides, and unites with the buccal cavity as already described. On the external surface of the sides of the labrum there is a row of short spines, where it is pressed against the labial gutter. At the distal end the labrum broadens out considerably, and is produced into two tubercles, which are fitted into corresponding shallow pits on the distal ends of the labral apodemes, this being the reverse of the method of union in the Muscidae. The apodemes are long and stout, and terminate at the proximal end in rounded points.

The hypopharynx is a very slender flattened organ, of the type seen in the Stomoxydinae, and contains the salivary duct between its two layers. At the upper end of the haustellum the flattened lateral areas are absorbed; the dorsal lamina fuses with the closed part of the epipharynx, the ventral with the labial gutter, while the salivary duct passes into a deep pocket-like recess in the middle of the latter.

The wall of the labium is composed of the mentum and the labial gutter, which serve about equally in rendering the proboscis a rigid piercing organ. The mentum in the bulb is composed of rather thin chitin, and is devoid of hairs. In the narrow part it is very thick and strong, and forms a shallow trough occupied mainly by a pair of tendons and some muscle fibres connecting it with the gutter. On its external surface there are two parallel rows of minute spines extending from the labellar area to the bulb; the hairs are arranged in pairs, the intervals between which diminish progressively as the bulb is approached. The labial gutter is a shallow trough of thick chitin, of almost as great a breadth as the mentum, to which it is connected by a narrow band of thick fibrous tissue. At the sides there is a ridge of chitin projecting downwards and slightly outwards, in line with the lateral margins, so as to give the gutter on section the appearance of a letter H, greatly elongated in the transverse diameter. The gutter is not depressed between the sides of the mentum, nor does it extend sufficiently far forwards to enclose the labrum-epipharynx. It is continued unchanged throughout the labellar region, but is slightly dilated at the distal end for the reception of the bases of the teeth.

Biting apparatus of Hippobosca

The cutting apparatus consists of a set of teeth at the prestomum, corresponding to the prestomal teeth in the Muscidae, a serrated ridge on the external surface of the labellum on each side, and a modification of the external wall which renders the distal portion capable of movement on the rest of the mentum. (Plate XIII, fig. 5.)

There are five prestomal teeth on each side, arranged in a radiate manner, the middle and largest tooth being directed straight forwards. Its distal end is bifid, with two equal arms, while in the teeth on either side of it the arm next the middle line is the largest. The proximal ends of the teeth are rounded, and are fitted into the dilated end of the labial gutter. The external set of teeth (Plate XIII, figs. 4 and 5) are flattened and typically serrate, with points directed upwards towards the head.

The distal end of the external wall of the labium is separated from the rest by a short interval of thin and flexible membrane, the margin proximal to which is a little thickened. The tendons which traverse the length of the labium, arising from the muscles of the bulb, are inserted into this separated area, so that a contraction of these muscles results in drawing the portion of the wall distal to the membrane upwards. This everts the prestomal teeth, and also draws the line of teeth on the external surface upwards through the wound, the method of action being in all essential points the same as that in *Glossina.* The teeth are thrust back into position for the next cut by the distension of the space between the wall in the labellar area and the labial gutter. These actions must, of course, be repeated with extreme rapidity.

The palps are elongate and ovoid in shape, and consist of a single joint. Their external surfaces are convex, and are beset with stout hairs, while the internal surfaces are flattened. The two are in close contact with one another in the position of rest, and are the only part of the apparatus which can be seen without dissection. On the inner surface of each there is a deep longitudinal gutter, the two gutters forming a canal in which the narrow part of the haustellum rests.

The membrane from which the palps arise is attached above to the distal edge of the clypeus, and corresponds to the anterior wall of the rostrum. But on account of the position of the haustellum, all of which, except that part which lies between the palps, is within the head in the position of rest, the membrane, in order to reach its attachment to the distal end of the haustellum, has to be invaginated within the head around the latter. In sections, therefore, the haustellum appears to be surrounded by a tube of membrane, which commences at the aperture behind the palps, and terminates by becoming attached to the distal end of the bulb.

The parts corresponding to the rostrum are provided with a musculature very closely resembling that of *Musca,* but having the bundles more clearly differentiated from one another than in that form (Plate XIII, fig. 3). The actions of the muscles are also the same, but the final result, instead of being a protrusion of the rostrum from the head and the extension of the whole proboscis, is only the protrusion of the haustellum from between the palps. The fulcrum is rotated on its attachment to the clypeus, so that the pharynx comes into line with the haustellum, and at the same time the buccal cavity which connects the two is straightened. In the resting position the buccal cavity is bent backwards in its lower part, on account of its length.

The wall of the head capsule is not thrust forward sufficiently in this species to justify the term rostrum, but the same sort of movement occurs. The invagination of the membrane around the haustellum is undone as the piercing stylet is thrust out between the diverging palps. (Plate XI, fig. 3.)

The relations of the muscles are so like those in *Musca* that the figure will explain itself.

INTERNAL STRUCTURES OF THE HEAD

The only internal structures connected with the exo-skeleton of the head in the Diptera are the intracranial tunnels and the ptilinum. The former occur only in the Orthorraphic flies, while the latter is characteristic of the Cyclorrappha.

Intracranial Tunnels

The *intracranial tunnels* (Plate IV, fig. 4) are probably homologous with the tentorium of other insects. They occur in all the blood-sucking Orthorrapha, and in many of the others. In most cases they are hollow tunnels, passing from the anterior to the posterior wall of the head capsule, and open at each end. They are bilateral, those of the two sides converging towards one another from behind forwards, on each side of the first part of the sucking apparatus and a little above it. The posterior opening is situated between the base of the proboscis and the occipital foramen, and the anterior at the side of the clypeus, below the antennae. The tunnel is generally narrowest in its middle position, and in some forms, as for instance *Simulium*, the lumen is closed at the narrowest point.

The function of these tunnels is to support the walls of the head cavity, and especially to enable them to resist the action of the powerful dilator muscles connected with the sucking apparatus. In *Tabanus* they are so placed as to transfer the strain of the muscles of the buccal cavity from the anterior to the posterior wall of the head, and, in order to distribute the strain over a wider area, the anterior end expands in a funnel-shaped manner. The posterior end is attached to a strong bar of chitin at the side of the membraneous area of the inferior wall, at the base of the proboscis. The fact that they are hollow has no more significance than that, weight for weight, a hollow cylinder is stronger than a solid rod.

The submental region, which in the Orthorraphic flies is mostly membraneous, is strengthened by the development of strong lateral bars of chitin, which are connected posteriorly with the occipital foramen. The foramen itself is strengthened and defined above by a thick arch of chitin, the extremities of which are turned outwards. The various portions of the margins of the foramen have received distinctive names, which are of little importance for the present purpose. The rigid nature of the margins of the foramen should be remembered when dissecting the part.

The Ptilinum

The *ptilinum* is characteristic of the Cyclorrapha, and is related to the method by which the imago emerges from the pupal case. The external opening, as already described, lies above and at the sides of the antennae, and is known as the *ptilinal suture*. From the margins of this orifice the wall of the head cavity is invaginated in the form of a much convoluted membraneous sac, the external walls of which are covered with scales of various shapes (Plate XVI, fig. 2) ; the internal surface of the membrane has attached to it a number of scattered muscle fibres. In sections the sac is found in the upper part of the head and in front of the brain; its wall is always thrown into very numerous folds, so that on a first examination one would hardly recognize it as a sac. In newly-hatched flies it can be easily evaginated as a rounded tumour by compressing the head with a needle.

The purpose of the ptilinal sac is to thrust off the end of the puparium at the moment the fly is ready to emerge, and this is accomplished by the distension of the sac with air, by respiratory movements of the body. The method of emergence, and the consequent presence of the ptilinal suture in the imago, are two of the essential features which separate the Cyclorrapha from the rest of the Diptera; the Orthorrapha do not escape by detaching the end of the pupal case as a circular cap, but through a T-shaped opening on the dorsal surface. It is this feature which has given the flies the name Cyclorrapha.

The Neck

The *neck* is always well demarcated in the Diptera. In most flies it is a simple membraneous tube connecting the head with the thorax, but in some Orthorraphic flies the membrane may be strengthened by small lateral plates of chitin. These, however, are never sufficiently well developed either to impart any rigidity to the neck, such as would enable the fly to use the muscular force of the body to thrust its mouth parts into a resistant layer, or to interfere with the free movements of the neck. The movements of the neck are not extensive, and are limited to the adaptation of the proboscis to the position requisite for feeding. They are brought about by certain ill-defined bundles of muscles running between the internal surface of the neck and the prothorax.

The structures which pass through the neck are numerous, and some knowledge of the anatomy of this region is of importance in dissection. When the head is separated from the body by traction these structures are exposed, and with care they can be separated from one another, and those not required cut off. In the first place, there are always two comparatively large tracheae, one on each side, passing from the thoracic spiracles to supply the head with air. On the inner side of these there is a pair of salivary ducts or the commencement of the glands. In the middle line there are, from the dorsal to the ventral side in order, a minute blood vessel, a prolongation of the dorsal heart, so small as to be only seen in the larger flies; the duct of the crop or oesophageal diverticulum,* and below it the oesophagus; and below this the nerve cord which connects the brain with the thoracic ganglia. A little experience with the larger flies enables one to distinguish between these by their size and colour, and in dissection it is always sound to cut away boldly all that is not required.

THE THORAX

Segmentation

The principles of the structure of the walls of the thorax have already been explained in the paragraph on the segmentation of the insect body. Briefly, the typical thorax should consist of three parts, each representing a segment, and termed the prothorax, mesothorax, and metathorax, respectively. The wall of each segment should be composed of a tergite or dorsal plate, a sternite or ventral plate which may be divided in the middle line, and two lateral or pleural plates, the episternum in contact with the sternite and the epimeron in contact with the tergite. But in such a highly-specialized group as the Diptera one would hardly expect to find a primitive arrangement persisting, and the relations of the parts are moreover profoundly altered by the great development of one pair of wings, especially since the majority of the Diptera are powerful flyers. Indeed, this factor, with the consequent necessity for adequate surface for muscle origin and insertion, has introduced so much change that it is a matter of the utmost difficulty to allocate the various sclerites to their original positions. The wings which have persisted are the mesothoracic pair, and in consequence the mesothorax has become greatly increased at the expense of the segments in front and behind it, until it now occupies by far the greater portion of the external wall. The prothorax

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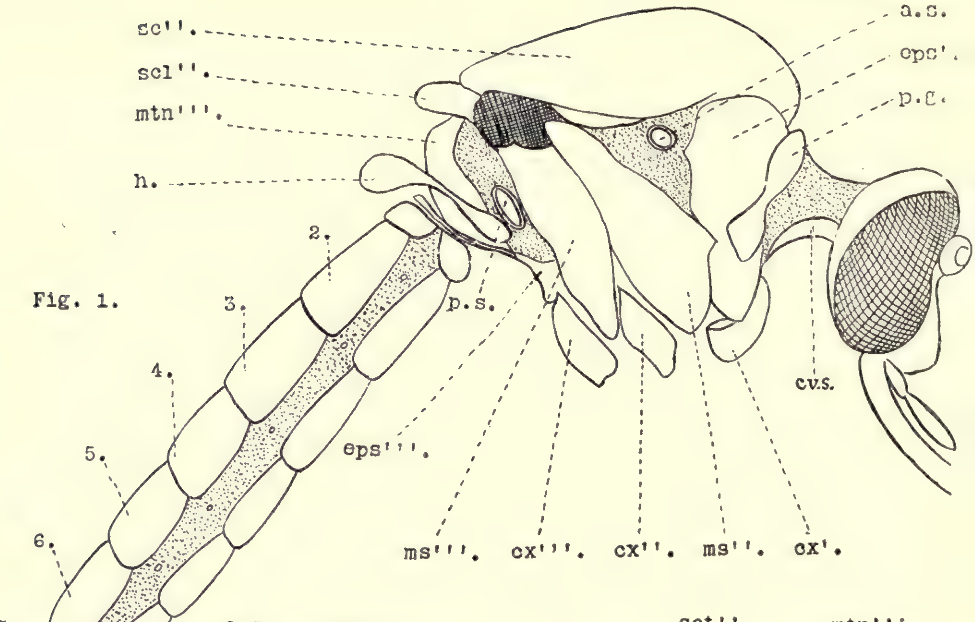
* In Musca and its allies the duct of the crop is ventral to the oesophagus.

PLATE. XIV.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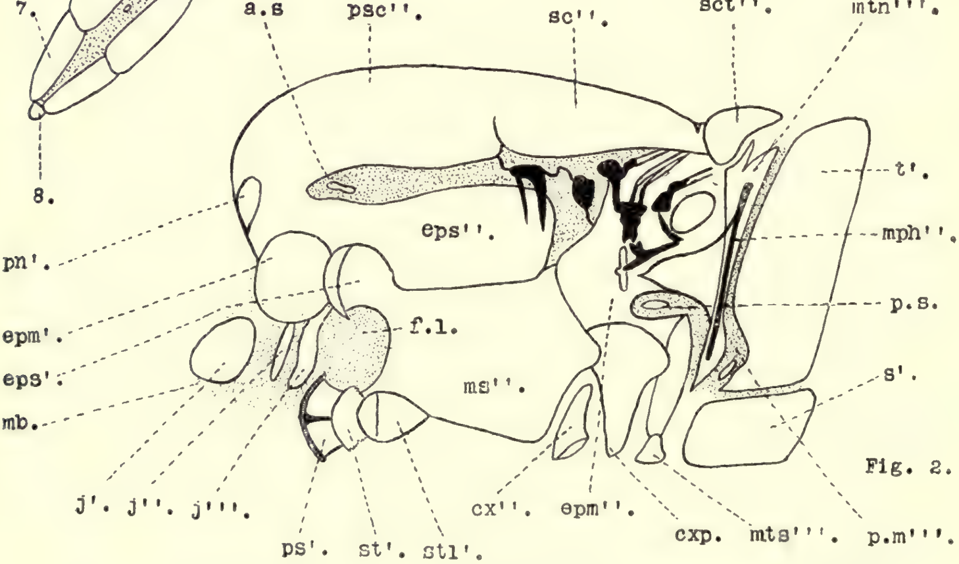
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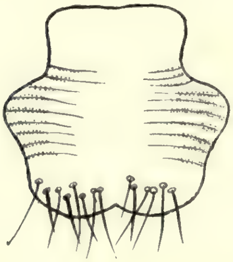
Fig. 2.



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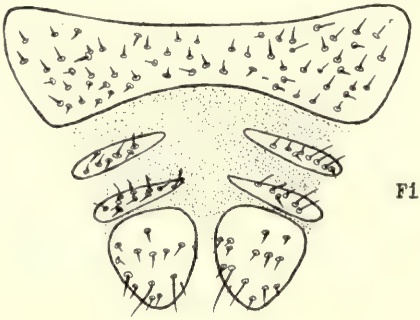

Fig. 4.

PLATE XIV

Figure 1. The parts of the exoskeleton of *Culex fatigans*. The dotted areas indicate soft membrane. The area of membrane at the wing base is shaded darkly. pg., patagia. eps′., episternum of prothorax. sc″., scutum of mesothorax. scl′., scutellum. mtn‴., metanotum (post scutellum, see page 74). h., halter. cv. s., cervical sclerite. cx′., cx″., cx‴., coxae of the three legs. ms″., mesosternum. The prosternum does not appear on the lateral wall. ms‴., the metasternum. eps‴., the episternum of the metathorax. a.s., anterior spiracle. p.s., posterior spiracle. The segments of the abdomen are numbered in order.

Figure 2. The thorax of *Tabanus albimedius*, seen from the inner aspect after dissection. pn′., pronotum. psc″., prescutum. t′., tergite of the first segment of the abdomen. s′., its sternite. epm′., epimerum of prothorax. eps′., episternum of prothorax. mb., membrane in the cervical region. j′., j″., j‴., the three jugular sclerites. f.l., the space for the articulation of the foreleg. ps′., presternum. st′., sternum of prothorax. stl′., sternellum. cxp., coxal plate. epm″., epimerum of mesothorax. mph″., mesophragma. Other letters as in Figure 1.

The sclerites controlling the movement of the wing are indicated, somewhat diagrammatically, in black.

Figure 3. The ventral plate of the ovipositor of *Haematopota pluvialis*. × 50.

Figure 4. The plates which make up the dorsal wall of the ovipositor of same. They are easily recognizable as degraded tergites of suppressed segments. × 50.

is reduced to a narrow ring into which the membrane of the neck is inserted, and the metathorax to a ring of only a little greater extent, uniting the thorax to the abdomen; on the dorsal surface in many forms the whole of the wall belongs to the mesothorax. The sutures between the various sclerites are generally close ones. In many cases the separation is only indicated by a ridge on the internal surface and a narrow groove externally, or sometimes only by a dome-like elevation on the outer wall. The whole thorax forms a chitinous box, opening anteriorly into the neck and posteriorly into the abdomen, and is filled up almost entirely by the powerful muscles of flight. The various structures which pass from the head to the abdomen lie in the ventral portion of the cavity, and occupy a very small amount of the space.

The difficulty that exists in attaching the correct names to the different parts will be readily appreciated when it is stated that there are in existence four drawings of the thorax of the house-fly by entomologists of note, no two of which are named in the same manner. Fortunately the subject is not of great practical importance, and it will suffice if the discussion is confined to the practical points which have to do with the dissection of the fly, and to the nomenclature in so far as the terms are used in systematic classification. With regard to the latter point a good deal of difficulty is met with, for the terms in use by systematists are frequently very vague so far as their reference to the same part in different flies is concerned.

The distribution of the various sclerites and the alteration in position which they may undergo will be best understood by studying a concrete instance first; the thorax of *Tabanus* will serve as an example, as it occupies a more or less intermediate position between the extremes. In this form the whole of the dorsal wall of the thorax as seen externally is formed by the tergite of the mesothorax, which is subdivided into several portions by more or less distinctly marked transverse fissures. About the middle of the thorax, and just anterior to the wing insertion, there is on each side a short fissure or notch which indents the margin. The part in front of this is the *praescutum*, and the part behind the *scutum*; the separation between the two is indistinct, and only marked by these lateral notches. Behind the scutum, which is somewhat narrowed posteriorly, there is a stout and conspicuous triangular piece termed the *scutellum*. This projects a little above the first segment of the abdomen, and is distinctly demarcated from the scutum by a transverse fissure. This is all that can be seen on the dorsal surface

Tabanus
(Plate XIV, fig. 2)

in pinned specimens, but if the thoracic wall is cleared in potash and dissected one finds at the anterior end two small elevations overhanging the neck and separated from one another in front by a narrow interval. These represent the two lateral halves of the tergite of the prothorax, and are termed the ***pronotum***, just as the tergite of the middle segment is known as the ***mesonotum***. The tergite of the metathorax, or the ***metanotum***, is represented by a narrow strip of chitin which arches from side to side under cover of the scutellum. On the ventral surface of the thorax all the segments are represented, and in addition there are some pieces which belong properly to the neck, but have become displaced backwards. Starting from the middle line in front, the area where the thorax joins the neck is occupied by a loose membrane which permits of free movement of the neck on the body, and also permits of a considerable amount of distension when blood is flowing through the oesophagus. In this membrane there are three pairs of sclerites, none of which are united in the middle line. The first pair are quite free in the membrane, the second and third pairs attached laterally to the side walls of the thorax. These are the ***jugular sclerites***, belonging to the neck. They are all small and oval in shape, and are not conspicuous on the external surface of the thorax, being concealed by the head. Behind them there are several sclerites closely pressed together and united in the middle line. These are differentiated portions of the sternite of the prothorax, and are termed the ***praesterna***, ***sternum***, and ***sternellum*** respectively. The praesterna are united in the middle line by a thick ridge, and together form a broad transverse plate with a thickened anterior border, which limits the thorax in front, and to which the membraneous neck is attached. The sternum is semi-circular in shape, and is wedged in behind and between the praesterna. Behind this there is the sternellum, a heart-shaped plate, closely fitted between the two sterna of the mesothorax. Arising from these divisions of the prosternite there is a complex arrangement of fibrous bands which serve to strengthen the walls of the thorax and to provide attachments for muscles; these will be referred to later.

The sternite of the mesothorax is divided only in the middle line, and consists of two large quadrilateral plates, which occupy about one-third of the total lateral area. The two plates join one another in the middle line at an acute angle, and so give the thorax a keeled appearance. Behind them there is a small oval plate representing the sternite of the metathorax, and behind this the first sternite of the abdominal wall.

The sclerites of the lateral wall are comparatively simple, and can be homologized with the primitive type. At the anterior end there are two dome-shaped elevations, one behind the other, conspicuous on the external surface on account of the prominent tufts of hairs which they bear. The most anterior of these is continuous with the dorsal wall, and lies just below the pronotum on each side; it may be taken to represent the *epimeron*, or dorso-lateral pleural plate. The *episternum*, or ventro-lateral plate, lies immediately behind it, and is continuous with the upper anterior angle of the mesosternum. Between it and the three divisions of the prosternum there is a comparatively wide interval, in which the first leg of each side is articulated; it is on account of this loose articulation that the fore legs have in all Diptera a wider range of movement than the other pairs. Behind these sclerites and above the mesosternum there is the *episternum* of the mesothorax, a large plate similar in shape to the mesosternum, but smaller. The *epimeron*, if the term may be used here, does not conform to the type with the same exactness. It is represented by a most irregularly shaped plate which extends from the insertion of the wing to the middle line ventrally, and connects the mesothorax with the metathorax. In its middle third it is firmly united to the upper half of the posterior border of the mesosternum, but above and below this part it is attached to the adjacent sclerites only by a membrane, leaving a wide interval below in which the second leg is inserted. Behind its somewhat irregular posterior border there is a narrow plate representing the fused pleural plates of the metathorax; these articulate posteriorly with the dorsal plate of the first segment of the abdomen, and are continuous above with the metanotum.

It will be noted from the above description that the wall of the thorax is formed from a large number of plates of different sizes and shapes, which are for the most part fitted closely to one another. They are, in fact, closely fused together to form a chitinous box, and cannot be separated by dissection. But at certain places the union is less firm, and expansion of the thoracic wall can and does take place. The most important of these regions is that between the mesonotum and the lateral wall, where there is a wide longitudinal fissure extending from the level of the epimeron of the prothorax to the insertion of the wing, and passing downwards between the posterior border of the meso-episternum and the anterior border of the upper third of the meso-epimeron. By virtue of this membraneous space the dorsal wall of the thorax is capable of a certain amount of movement on the lateral walls. The membraneous area at the junction of the thorax with the neck has already been noted. Posteriorly there is a more restricted area between the meso-epimeron and the meta-pleural plate, and another narrow strip running vertically down the wall, between the posterior margin of the thorax and the abdomen.

Endo-skeleton of Thorax

On the internal aspect of the thoracic wall there are certain chitinous structures which are termed collectively the endo-skeleton; they are, of course, mere ingrowths from the exo-skeleton, and are designed to afford attachment for the muscles and to give additional stability to the wall. In the prothorax the existence of such a structure has already been mentioned (Plate XV, fig. 6). It consists of two strong fibrous bands which run outwards and forwards from the sternite to the pleural plates, binding the whole together and serving to compensate for the looseness of the wall in the region of the attachment of the neck. The anterior of these is a broad and thick transverse band which arises from the whole length of the line between the praesterna and the sternum, and forms a wide arch parallel to and behind the borders of the latter. Laterally it terminates in a stout rounded cord. The posterior part arises from the lateral borders of the sternellum, and contracts to a similar cord, the two uniting above the articulation of the fore leg. The fibrous band so formed spreads out in a fan-shaped manner, and becomes continuous with the anterior and internal edges of the episternum of the prothorax, which are turned inwards and backwards to meet it.

In the mesothorax there is a structure of a different kind, designed solely for the attachment of muscles. It consists (Plate XV, fig. 4) of a pair of wing-like expansions set on a Y-shaped stalk, which lies in the groove between the two lateral divisions of the mesosternum. Each expansion consists of two thin plates of chitin, separated from one another behind by a smaller plate perpendicular to them, but converging towards one another anteriorly, so that they form the boundaries of a boat shaped cavity. Behind the large anterior cavity there is a smaller one, the anterior boundary of which is formed by the same transverse plate which forms the posterior limit of the anterior cavity. Important muscles arise from the inner surfaces of these plates, and the structures which pass through the thorax rest between the arms of the Y-shaped strand of chitin to which they are attached.

In the mesothorax there is a much more important structure, the *mesophragma* (Plate XV, fig. 1), which forms a most formidable obstacle

PLATE XV

Figure 1. The thorax of *Chrysops dispar*, seen from behind, to show the mesophragma. mtn‴., the metanotum. h., halter. p.s., posterior spiracle. p.f., post-furca. cx‴., coxa of the third leg. th.o., thoracic outlet, through which the organs pass to the abdomen. mph., mesophragma. × 28.

Figure 2. A halter of *Chrysops dispar*. × 70.

Figure 3. The tarsus and foot of *Haematopota pluvialis*. The empodium is pulvilliform. × 66.

Figure 4. The apodeme of the mesothorax of *Tabanus albimedius*, or the medifurca. × 90.

Figure 5. The foot of *Culex fatigans*. Note the flange on the proximal part of the claw. × 500.

Figure 6. The prosternal region of *Haematopota pluvialis*, seen from the inside. ps′., the presternum. st′., the sternum. epm′., the epimeron. eps′., the episternum. stl′., the sternellum. a.f., the anterior fibres, and p.f., the posterior fibres, which run to the side walls of the thorax. f.l., space for the articulation of the foreleg. × 90.

Figure 7. A leg, to show the divisions. cx., coxa. tr., trochanter. fe., femur. tb., tibia. mt., metatarsus. t., tarsus.

PLATE. XV.

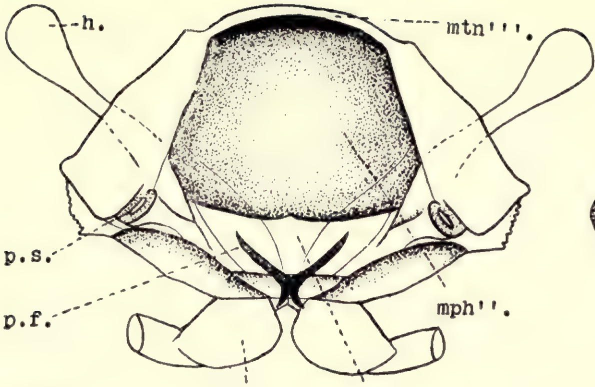
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Fig. 1.

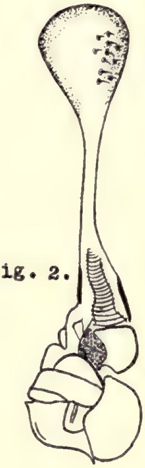
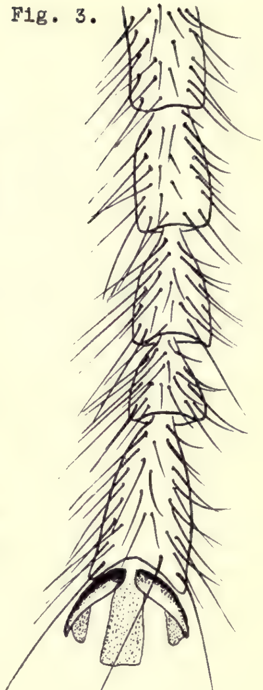
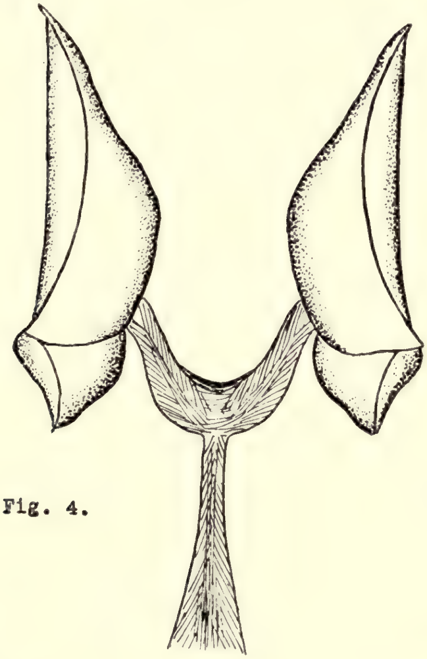


Fig. 2.

Fig. 3.





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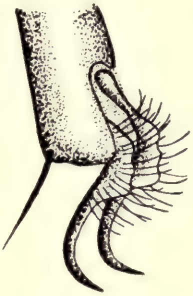

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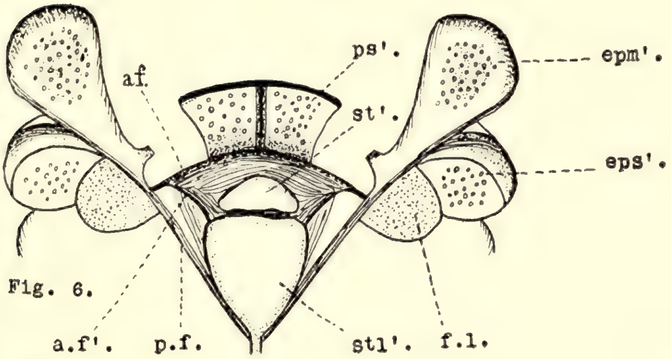
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Fig. 6.

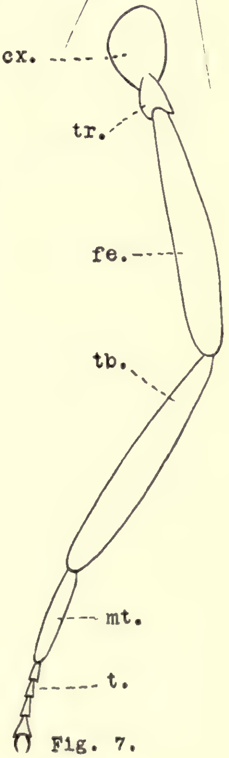
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Fig. 7.

in the dissection of the Tabanid flies. It consists of a wide arched sheet of chitin, arising from the upper part of the meso-epimera on each side, and also from the dorsal wall of the thorax; this extends inwards and backwards through the metathorax to reach as far as the posterior limit of the latter, the chitin from the two sides meeting in the middle line to form one continuous sheet, which thus cuts off the upper portion of the thoracic cavity from the abdomen, and leaves only a narrow interval. All the structures which pass from the thorax to the abdomen have to pass through this aperture. The purpose of this diaphragm is to afford additional surface for the attachment of the powerful muscles which provide the motive power for flight.

Mesophragma

The metathorax has an apodeme similar to that of the mesothorax, lying upon the metasternum. It consists, however, of only one sheet of chitin on each side. The sheets are pointed and wing-like, and are supported by strong ribs of chitin, which converge posteriorly towards one another, and again diverge to form a pair of stout hooked processes. The structure lies immediately behind the third pair of legs.

The three structures in the middle ventral line are sometimes termed the *ante-*, *medi-*, and *post-furca*, respectively. Similar structures are found in most insects. The mesophragma is specially well developed in the Tabanidae, but some arrangement of the kind is found in all Diptera.

Sclerites of Wing base

On the internal surface of the thoracic region there are to be found some interesting sclerites which control the movements of the wing. In *Tabanus* (Plate XIV, fig. 2) there are two distinct sets, an anterior and a posterior. The anterior set consists of three conical sclerites attached to one another by a fibrous cord running between their broad upper ends, and stretching from the dorsal plate, just anterior to the fissure separating the praescutum from the scutum, to the free part of the upper border of the meso-epimeron. When the muscles attached to these sclerites contract the longitudinal fissure across which they stretch is narrowed and the vertical diameter of the thorax reduced. The posterior set consists of five very irregularly shaped sclerites, which are so articulated with one another, and which have their movements so co-ordinated, that when the wing is folded the squama is folded on the rest of the wing, while when it is extended the whole of the wing is brought into one plane. The three upper sclerites are continuous with the bases of the three principal veins of the wing, and the fourth with the squama itself; as will be seen from the figure, when the longitudinal rod at the bottom of this system of levers is rotated upwards on the fixed point at its anterior end, the wing is folded and the squama rotated in a direction opposite to the base of the wing, while when it is rotated downwards the squama is pushed in the opposite direction, that is, into the same plane as the rest of the wing.

Taking *Tabanus* as a type the composition of the thorax in the Culicidae and the Muscidae, representing simpler and more complex arrangements respectively, may be discussed briefly.

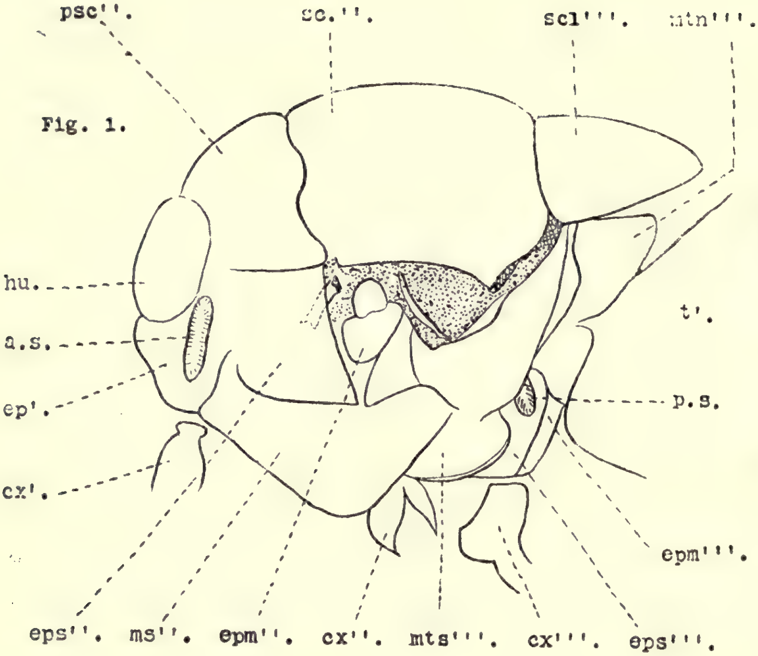
Mosquito

In the mosquitoes (Plate XIV, fig. 1), as one would expect in creatures of less powerful flight, the sclerites are composed of thinner and less rigid chitin. The thorax is less compact, longer in proportion to its breadth, and more pointed in the middle line ventrally, than that of *Tabanus*. The three pairs of legs are also attached nearer together, and appear to arise, to use the words of Nuttall and Shipley, from the apex of a pyramid. The disposition of the sclerites is indicated in the figure. The prothorax is reduced, though not nearly to so great an extent as in *Tabanus*, and consists of a large lateral plate, the episternum, and a small sternum which can only be recognized on dissection. The episterna are articulated to the cervical sclerites, and there is in this form also a comparatively wide membraneous area at the base of the neck, which can be seen to bulge when the mosquito is feeding. The episterna occupy a considerable part of the wall of the thorax, and extend as far as the first pair of legs. They bear near their anterior borders the curious structures known as the *patagia*. These are sausage-shaped bodies, distinctly elevated above the surface, and connected internally with the prosterna by fibrous bands, in the same manner as the epimera of the Tabanids are connected with the sterna and sternella. The membraneous interval between the dorsal and lateral walls of the thorax is triangular, and lies between the mesosternum and the lateral plate of the prosternum. There is also a rather wide interval between the mesothorax and the metathorax.

One point which should be particularly noted in the anatomy of the thorax of the mosquito is that there are two elevations posterior to the scutum. The first of these is by common consent called the scutellum, the second, which is hidden underneath the first when the thorax is seen from above, is the post-scutellum, a part of the dorsal wall of the mesothorax. This latter piece is referred to by Theobald as the metanotum, but this is incorrect, for, as pointed out by Nuttall and Shipley, there is a narrow slip posterior to this which is the true dorsal

PLATE XVI.

Fig. 1.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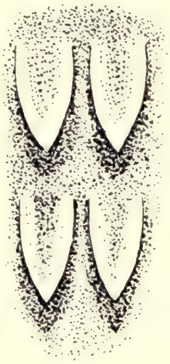

Fig. 2.

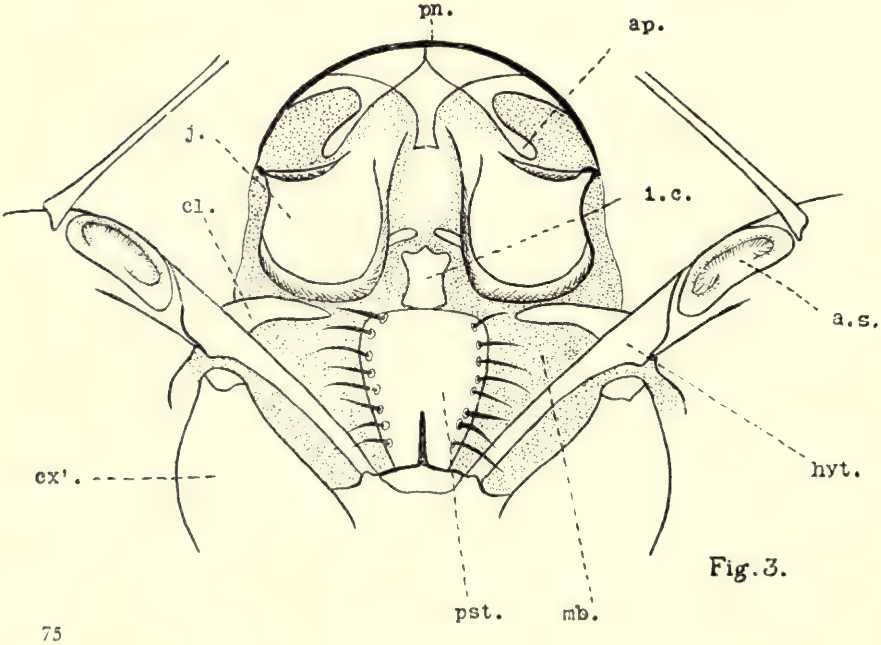
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Fig. 3.

PLATE XVI

Figure 1. The thorax of *Stomoxys calcitrans.* hu., humerus. psc″., the prescutum. sc., the scutum. scl., scutellum. mtn″., metanotum. t′., tergite of the first abdominal segment. a.s., anterior spiracle. ep′., episternum of prothorax. eps″., episternum of mesothorax. cx′., cx″., cx‴., coxae of the three pairs of legs. ms″., mesosternum. epm″., epimeron of mesothorax. mts‴., metasternum. eps‴., episternum of metathorax. epm‴., epimeron of metathorax, or lateral plate of the metasternum. p.s., posterior spiracle. × 25 approx.

Figure 2. The scales on the ptilinal membrane of *Philaematomyia insignis.* × 1000 approx.

Figure 3. The thoracic inlet of *Stomoxys calcitrans*, seen from the inside. pn., pronotum. ap., apodeme. j., jugular sclerite. cl., clavicle. cx′., coxa of the first leg. i.c., interclavicle. a.s., anterior spiracle. hyt., hypotreme. mb., membrane. pst., prosternum. × 60.

It should be noted, as a guide in dissection, that the ventral margin of the inlet is much less rigid than the dorsal. The prosternum can be bent on its attachment.

plate of the metathorax, and should be termed the metanotum. The point is of importance from the systematic point of view, as most writers have followed the nomenclature of Theobald when describing species.

Stomoxys (Plate XVI)

In the Muscid flies the thorax is much rounder and more compact than it is in *Tabanus*, and is without a definite 'keel' to the ventral surface. The various parts are so welded together, and the various authorities hold such divergent views regarding the homology of the different sclerites, that it would be hopeless to attempt to give an acceptable account of the subject within a short space. The main divisions are, however, easily recognized. The whole of the dorsal wall as seen externally belongs to the mesothorax. It is divided about the middle by a deep transverse fissure, the anterior part, as in *Tabanus*, being the praescutum, and the posterior the scutum. Posterior to this there is the scutellum, like that of *Tabanus*, but generally more conspicuous and pointed. The ventral surface is almost entirely occupied by two large quadrilateral plates, the mesosterna ; behind these there are several irregularly shaped plates belonging to the metathorax. On the anterior aspect of the thorax there are two prominent convexities between the praescutum and the anterior end of the sternum, which represent the pronotum. On the lateral aspect there are two plates between the dorsal wall and the sternum ; the anterior of these is the episternum, and the posterior the epimeron, of the mesothorax. These are separated from one another by a conspicuous vertical suture. In the space anterior to and below the wing base, and in the angle between the episternum and the epimeron, there are several small sclerites, one of which is specially distinguished as the tegula.*

The internal structure of the thorax resembles in general that of *Tabanus*. The thoracic inlet has, however, more definite boundaries, and the fibrous bands which unite the median and lateral walls behind the neck are well developed, and are here termed the ***hypotremes***. There is a medi-furca resembling that of *Tabanus*, a small post-furca, and a mesophragma, though this is not nearly so well developed as in the Tabanidae.

From the foregoing it will be evident to the reader that the terminology of the thorax is at present in an unsatisfactory state, and must remain so until a great deal of attention has been devoted to the subject. Nevertheless, some settled method of nomenclature is a necessity in descriptive work, in order to be able to denote with some degree of accuracy the positions of bristles, markings, etc., by means of which many species are identified. Terms which have a strict anatomical significance can only be applied where the homology of the part has been determined with reasonable certainty, and cannot, however desirable it would be from the purely scientific point of view, be applied in the present state of our knowledge. To meet this difficulty a nomenclature has been adopted, and is now in general use among systematists, which is essentially conventional, and in the use of which no anatomical definition is implied. As Osten Sacken pointed out, such a conventional terminology has the great advantage of offering more chances of fixity, and can well exist side by side with a more purely anatomical one, which must necessarily be modified as our knowledge of the structure of the Diptera increases.

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* This term is applied by some writers to a division of the wing base.

It is chiefly among the higher Diptera that difficulties are met with, as in the description of these it is often essential to define with precision the positions of the large bristles or macrochaetae. Chaetotaxy will be dealt with later, but before doing so it will be necessary to describe the various regions in the current terms. The definitions given by Osten Sacken, who was the first to emphasise the importance of the subject in descriptive work, will be followed almost verbatim, as his paper, published in 1884, is not readily accessible, and contains an authoritative account. At the same time the terms employed will, as far as possible, be brought into line with those which have been used in the foregoing pages, using *Stomoxys*, of which a figure is given on Plate XVI, as a type. (See also Plate XIX, fig. 6.)

Nomenclature of Thorax

The sutures which separate the various plates from one another are used as landmarks. Thus, the *dorsopleural* suture runs from the humerus to the root of the wing, and separates the mesonotum (or tergum) from the pleura. The *sternopleural* suture is horizontal, and lies below the dorsopleural and parallel to it. The *mesopleural* suture runs downwards from the wing, and separates the mesopleura from the pteropleura. The *mesopleura* lie between the dorsopleural and sternopleural sutures, and therefore correspond to the episternum of the mesothorax, as indicated in the figure. The *pteropleura* are situated under the insertions of the wings and behind the mesopleural sutures. In the figure the region will be seen to lie between the membraneous area at the wing base and the posterior spiracle. It corresponds to the lateral plate of the mesothorax of Lowne, the same term being employed by Gordon Hewitt in his description of *Musca domestica.* The *sternopleura* are defined as those portions of the mesosternum which, from their position, form a part of the pleura, or side walls of the thorax, in contradistinction to the middle portion of the mesosternum. The *hypopleura* are distinct pieces above the two last pairs of coxae, and behind the sternopleura, from which they are separated by sutures. The region is shown in *Stomoxys* as the metasternum. The parts in this region are much compressed together, and the separate sclerites are difficult to define. The *metapleura* lie immediately above the hypopleura, and behind the pteropleura; this region is more or less convex, and lies between the root of the wing and the halter. Other terms in use are as follows. *Scutellar bridges*—small ligaments on either side of the scutellum which connect it with the mesonotum. *Praesutural depression*—a depression lying in the angle between the transverse suture on the thorax (between the scutum and praescutum), and the dorsopleural suture. *Praealar callus*—a more or less distinct tubercle in front of the root of the wing, and *Postalar callus*, a similar tubercle behind the wing, between it and the scutellum. The *humerus*, or *humeral callus*, is usually a well-marked convexity at each side of the anterior end of the thorax, and corresponds to the pronotum.

THE WINGS (PLATE XVII)

The possession of only one pair of wings, the mesothoracic, is characteristic of the Diptera, and, as is to be expected in insects of such powerful flight, they are highly developed.

A word as to the origin of the wings. They are not appendages in the zoological sense, but arise as outgrowths from the body wall, formed in the pupal stage. The small buds which first appear become gradually flattened out, and as they grow their substance is penetrated by tracheae or air tubes, which, when the wing has assumed its final leaf-like form, remain as veins or nervures to support the delicate membraneous portion.

The wings do not vary much in shape in the different families. The anterior border is straight or nearly so, the apex and posterior border gently rounded. The posterior border is generally indented in such a way as to divide the wing in this region into parts which have received distinctive names. The indentations are found in the proximal half, and are known, from without inwards, as the *anal lobe*, (so called because when the wings are folded this portion of the wing lies over the distal end of the abdomen*) the *alula*, the *antisquama*, and the

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* This is not always actually the case.

squama. The last named is generally a distinct portion of the wing, and is much thicker and coarser than the rest, and has often a fringe of fine hairs around its border; it is separated from the wing except at one point, and is folded underneath in repose, so as to be in contact with the antisquama, this being accomplished by a mechanism such as that described when dealing with the anatomy of the thorax of *Tabanus*.

The wings may be simple, transparent, and more or less iridescent, in which case it is usual to find a row or rows of short but stout spines on the principal veins, or their surface may be mottled in various ways, as in *Haematopota*. The veins may have no other coating than the rows of spines, or they may bear scales of various sorts, as in the Culicinae. The scales may be all of one colour, as in the *Culex* group, or they may be variously coloured, and impart to the wing the dappled appearance which is characteristic of the *Anopheles* mosquitoes. In *Phlebotomus* they are covered with a dense layer of fine hairs.

Venation

The veins of the wing present great and important variations in the different families, and the venation is, by common consent among dipterologists, regarded as one of the most important factors in deciding systematic position. As a general rule the more primitive the form the more equally will the wing veins be distributed over the surface, and the more advanced then the more will they be concentrated towards the anterior border, the most anterior veins of all becoming shorter and joining the anterior margin of the wing at a more proximal point. The veins radiate from the narrow base, where they are continuous with the sclerites which control the movements of the wing. The longitudinal veins are here and there united by short cross-veins, and, with these and the margins of the wing, the whole area is divided into a number of spaces called cells. As the veins are crowded to the anterior border the more anterior of these cells become reduced in a corresponding degree, the posterior part of the wing being left clear.

Several systems of nomenclature have been devised with regard to the veins, two of which are in common use at the present time; one of these has the advantage of ease of application and has up to the present time been the most used of any, while the other, that of Comstock and Needham, has the greater scientific value in that it attempts to bring the Diptera into line with other insects. It is probable that in the future it will replace the older method.

Comstock and Needham's Nomenclature

Comstock and Needham's system may be taken first, as being the most easily understood, though not necessarily the most easily applied. These workers deduced from an extensive series of observations a primitive condition of the venation, which they put forward as a 'urotype' (Plate XVII, fig. 1). In such a wing all the veins are to be traced to two tracheae, which enter the wing on the anterior and posterior borders respectively. Each of these divides at once on entering the wing to form a number of branches which traverse the long axis and ultimately reach the borders. In the fully formed wing these tracheae remain as the longitudinal veins, of which there are four derived from each trachea. Taking those from the anterior tracheae first, they are named in order from before backwards the costa, subcosta, radius and media. The *costa* is undivided, and lies near the anterior border of the wing. The *subcosta* bifurcates near its termination, both branches reaching the border anterior to the apex. The *radius* divides in the proximal third of the wing into two branches, the anterior one of which is continued undivided to the apex of the wing; the posterior divides twice, so as to produce four branches, all of which reach the wing margin near the apex. The *media* divides into two about the middle of the wing, and each branch again divides in the outer third, so that there are four terminal branches. The posterior trachea also gives rise to four veins. The first of these is the *cubitus*, which divides into two about the middle of the wing, each vein so produced running undivided to the posterior border. The remaining veins are simple and undivided, and are termed the *first*, *second* and *third anal veins*.

The types of venation seen in modern Diptera are derived from the urotype by coalescence of certain of the original veins with one another, and by the development of certain cross-veins. These unite the longitudinal veins with one another, and, with the wing borders, divide up the wing into areas known as cells. The difficulty in the application of this system is to determine which veins have coalesced when the number is reduced.

The veins and cells are distinguished by the initial letter of the primary vein from which they spring, followed by the numeral indicating the position of the branch, starting from the anterior side. Thus the first radial vein is *R1*, the second *R2*, the first division of the cubital vein *Cu1*, and so on. The cells are distinguished by the initial letter of the vein forming the anterior margin, preceded by the corresponding cardinal number. Thus, *3rd* R indicates the third radial cell, *2nd Cu* the second cubital cell, and so on.

The form which approaches the urotype the most closely is *Phlebotomus*. In the Culicidae and Tabanidae there is rather more concentration of the veins, but in all the Orthorrapha one finds them distributed more or less equally all over the surface. In the Cyclorraphic flies the concentration is marked, and in the Hippoboscidae the posterior half is almost free from veins, those derived from the posterior tracheae having become very much reduced.

The cross-veins which unite the longitudinal ones are placed and named as follows. The *humeral cross-vein* connects the costa and subcosta near the base of the wing. The *axillary vein*, generally thick but short, connects the veins of the anterior set at the insertion of the wing. The *radial-median vein* connects the fifth branch of the radial vein with the first division of the median vein. The *median cross-vein* connects the anterior and posterior divisions of the median vein with one another. The *median-cubital vein* runs between the fourth branch of the median vein and the first cubital.

The older Nomenclature

The older system of nomenclature is entirely empirical, and can only be applied to the Diptera. In it the veins are numbered and named in order from before backwards. The *costa* is the vein forming the anterior boundary of the wing, and is often continuous around the apex with the posterior border. The *auxiliary vein* or the *subcosta* lies behind it, and turns upwards to join it before reaching the apex of the wing. Then come in order the *first, second* and *third longitudinal veins*, arising from a common stem (the anterior trachea of Comstock and Needham's nomenclature), and behind them the *fourth* and *fifth longitudinal veins*, arising by a common stem corresponding to the posterior trachea. Behind these there is a *sixth*, and in some cases a *seventh, longitudinal vein*, which go to the posterior margin of the wing and correspond to the anal veins. The cross-veins are named as follows. The *humeral cross-vein* corresponds to that of Comstock and Needham's nomenclature. The *anterior, small*, or *middle cross-vein* unites the third and fourth longitudinal veins, the *posterior* or *lower cross-vein* the fourth and fifth, and the *upper* or *supernumary cross-vein* the second and third. The cells into which the wing is divided are named more or less in accordance with their position. Commencing at the anterior border, the *costal cell* lies between the costa and subcosta. The *subcostal cell* lies between the subcostal vein and the first longitudinal vein. The *marginal cell* lies between the first and second, the *first submarginal* between the second and third longitudinal veins, and the *second submarginal* between the two divisions of the third longitudinal. The *discal cell*, when present, is bounded by the fourth longitudinal vein, and forms a convenient landmark from which to commence studying the venation. Unfortunately, and this is one of the objections to this system of nomenclature, a discal cell is defined as one in which the boundaries are formed by veins alone and not partly by the wing margin, and the cell answering to this description in one fly may not always correspond with that in another in its relations to the veins. Along the posterior border of the wing there may be one or several cells, called the *posterior cells* and numbered from without inwards. They are bounded by the posterior margin of the wing and the divisions of the fourth and fifth longitudinal veins. Near the base of the wing there may be two cells, limited externally by the anterior and posterior cross-veins, and known as the *first* and *second basal cells*. The *anal cell* lies between the fifth and sixth longitudinal veins, and the *axillary cell* between the last longitudinal vein and the wing base, and corresponds to the anal lobe.

Certain other descriptive terms are in common use. When a cell is bounded externally by the wing margin it is said to be open, and when enclosed by the convergence of its two sides it is said to be closed. A cell formed by the bifurcation of a vein, and therefore more or less triangular in shape, is called a *forked cell*. The posterior basal cells are sometimes termed the first, second, and third forked cells, as for instance in most descriptions of mosquitoes.

Notwithstanding the great deviations from the type which are found in the various families, these systems of nomenclature are not so difficult to work out as would appear from the foregoing account. With the aid of an example of each, and of the accompanying figures, the reader should be able to work out the venation in any of the other families.

Venation of Mosquito

In most descriptions of mosquitoes the older nomenclature is used, and the wing of *Anopheles* (Plate XVII, fig. 2) may be taken as an example of this method. The costa, which forms the anterior boundary and is continuous around the apex with the thickened posterior border of the wing, presents no difficulty, nor does the auxillary vein behind it. The first longitudinal vein runs straight from the base to the apex of the wing, without dividing. At the base of the wing another vein arises just below it, and runs to the distal part of the posterior border, and there divides into two. About the middle of the wing there are two other long veins, which are not directly connected with the wing base; one of these arises from the first long vein and the other independently. These are, therefore, the second, third and fourth long veins. Behind them in the proximal part of the wing there are two other long veins, the anterior one of which bifurcates, while the other does not. These are the fifth and sixth veins. Those of the veins which bifurcate produce forked cells named according to their position. The anterior forked cell is enclosed by the two divisions of the second long vein, and the first and second posterior forked cells by the branches of the fourth and fifth veins respectively. The humeral and axillary cross-veins are not present, and there is no discal cell. The upper and middle cross-veins are nearly in line with one another, and connect the third long vein with those in front of and behind it, a short distance distal to its origin and about the middle of the wing. The positions of the junction between the costa and the auxiliary vein, the relative positions of the forked cells, and the point where the fifth vein cuts the margin, are of importance in classification.

Venation of Haematopota

The venation of *Haematopota* (Plate XVII, fig. 3) will serve as an example of the application of Comstock and Needham's classification. The costa is conspicuous at the anterior margin, and the subcosta arises in common with the vein behind and joins the costa after a very short course. The strongest vein in the wing lies next behind, and is only separated from the costa by a narrow interval; it gives off a branch internal to the middle of the wing, and then divides into two; the lower of the two divisions so formed again divides, so that there are altogether four divisions of the radial vein at the wing margin. Of these the second represents the second and third divisions, the vein having failed to bifurcate as it does in the urotype. The bifurcation of the lowest division into the fourth and fifth is peculiar, as the upper branch leaves the lower at a wide angle, and then immediately turns outwards, so that the two veins are parallel for a short distance instead of divergent. At the point where the fourth vein turns outwards there is a projecting spur, which points inwards. Behind the main stem of the radial vein there is another vein, which bifurcates about the middle of the wing. The two branches so formed converge a little towards one another about the middle of their length, and are connected by a cross-vein, thus enclosing a discal cell; the branch on the distal side bifurcates at the level of the cross-vein, and there are thus three divisions of the

PLATE XVII

Wing Venation

Figure 1. Comstock and Needham's Urotype.
Figure 2. *Anopheles.*
Figure 3. *Haematopota.*
Figure 4. *Stomoxys.*
Figure 5. *Glossina.*

Reference Letters

COMSTOCK AND NEEDHAM'S NOMENCLATURE

C.	Costa.
Sc.	Subcosta.
R1–R5.	The five divisions of the Radial vein.
M1–M4.	The four divisions of the Median vein.
Cu1 and Cu2.	The two divisions of the Cubital vein.
An1–An3.	The three anal veins.
r.m.	The radial median cross-vein.
m.cu.	The median cubital cross-vein.
cu.an.	The cubital anal cross-vein.

The cells are indicated by the initial letter of the vein in front of them, preceded by the cardinal number. Thus, 3rdR., the third radial cell.

THE OLDER NOMENCLATURE

The Veins

C., Sc.,	Costal and subcostal veins. The latter is also termed the auxiliary vein.
1 L—6 L.	The longitudinal veins.
a.c.v.	Anterior, upper, or supernumerary cross-vein.
m.c.v.	The middle cross-vein. The vein given this name in mosquitoes corresponds to the anterior cross-vein in *Stomoxys*, etc., and is the radial median vein. The anterior cross-vein, so called, is a supernumerary cross-vein between the second division of the radial vein and the one posterior to it.
p.c.v.	Posterior or lower cross-vein.
h.	Humeral cross-vein.
ax.	Axillary vein.
a.b.c.v.	Anterior basal cross-vein.
p.b.c.v.	Posterior basal cross-vein.

The Cells

c.c.	The costal cell.
sc.c.	The subcostal cell.
1st m.c.	The first marginal cell.
2nd m.c.	The second marginal cell.
sm.c.	The submarginal cell.
2 sm.c.	The second submarginal cell.
1 p.c.	The first posterior cell.
2 p.c.	The second posterior cell, anterior forked cell, first posterior forked cell.
3 p.c.	Third posterior cell.
4 p.c.	Fourth posterior cell, second posterior forked cell.
1 b.c.	First basal cell.
2 b.c.	Second basal cell.
d.c.	Discal cell.
an.c.	Anal cell.

Lobes of the wing

an.	Anal lobe.
al.	Alula.
as.	Antisquama, or antitegula.
sq.	Squama, or tegula.

PLATE XVII.

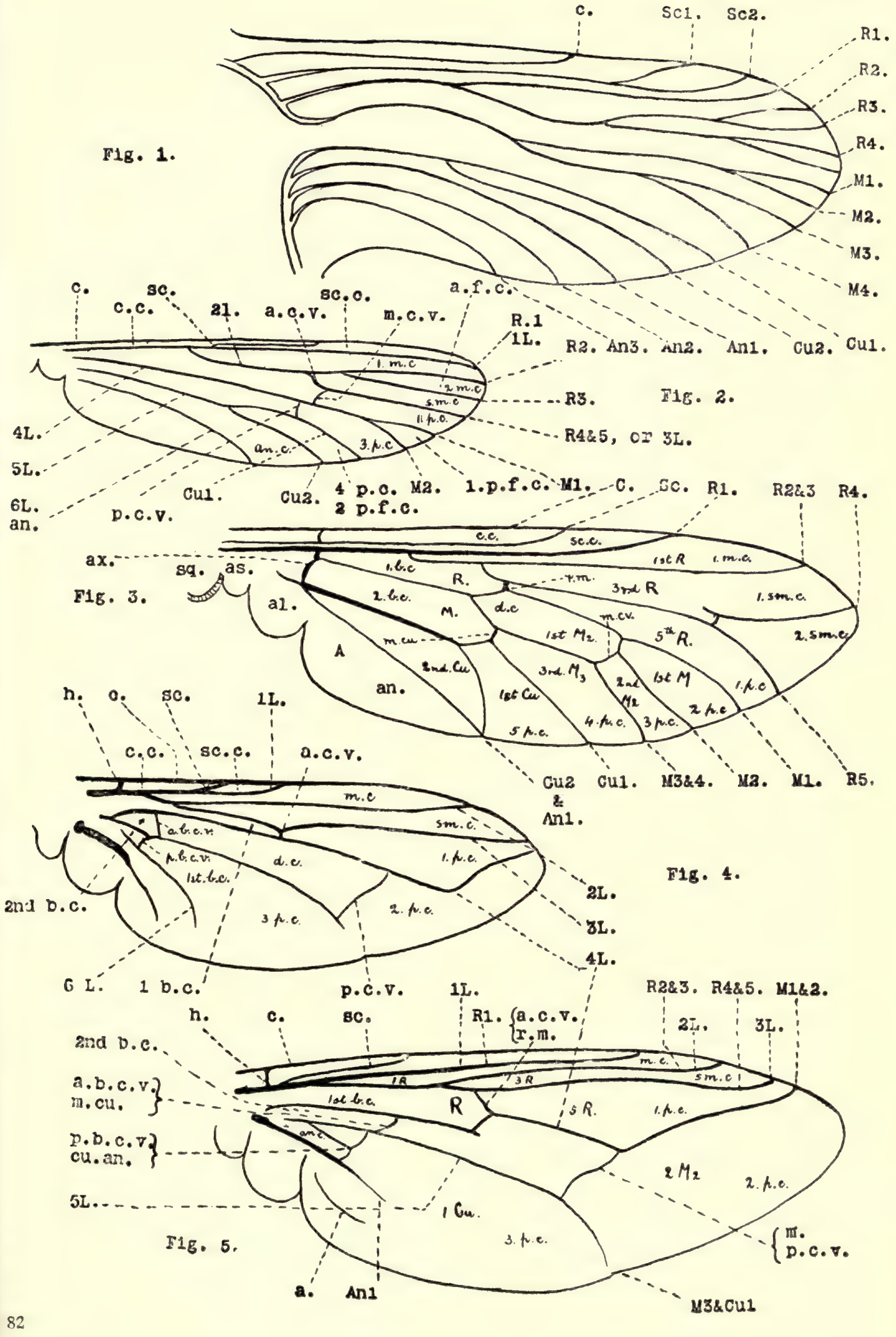


Fig. 1.
c.
Sc1.
Sc2.
R1.
R2.
R3.
R4.
M1.
M2.
M3.
M4.
Cu1.
Cu2.
An1.
An2.
An3.
R2.
Fig. 2.
c.
c.c.
sc.
21.
a.c.v.
sc.c.
m.c.v.
a.f.c.
R.1
1L.
1.m.c
2.m.c
s.m.c
1.p.c.
an.c.
3.p.c
R3.
R4&5, or 3L.
4L.
5L.
6L.
an.
p.c.v.
Cu1.
Cu2.
4 p.c.
2 p.f.c.
M2.
1.p.f.c.
M1.
Fig. 3.
C.
Sc.
R1.
R2&3
R4.
ax.
sq.
as.
al.
c.c.
sc.c.
1st R
1.m.c.
1.b.c
R.
r.m.
3rd R
1.sm.c.
2.b.c.
M.
d.c
m.cv.
2.sm.c
A
m.cu
1st M2
5th R.
an.
2nd Cu
3rd M3
2nd M2
1st M
1.p.c
1st Cu
4.p.c.
3 p.c.
2 p.c
5 p.c.
Cu2 & An1.
Cu1.
M3&4.
M2.
M1.
R5.
Fig. 4.
h.
c.
sc.
1L.
c.c.
sc.c.
a.c.v.
m.c
sm.c.
a.b.c.v.
p.b.c.v.
d.c.
1.p.c.
1st.b.c.
2nd b.c.
3 p.c.
2. p.c.
2L.
3L.
4L.
6 L.
1 b.c.
p.c.v.
Fig. 5.
h.
c.
sc.
1L.
R1.
a.c.v.
r.m.
R2&3.
R4&5.
M1&2.
2L.
3L.
2nd b.c.
m.c.
1R
3R
sm.c
a.b.c.v.
m.cu.
1st b.c.
R
5R.
1.p.c.
p.b.c.v.
cu.an.
an.c.
2 M2
2.p.c.
5L.
1 Cu.
3.p.c.
m.
p.c.v.
a.
An1
M3&Cu1

median vein at the wing margin; the proximal one of these, not having divided as it does in the urotype, represents the third and fourth. The cubital vein arises just below the median, but is not connected with it; it divides at a point just behind the first bifurcation of the median vein, the two branches proceeding direct to the wing margin; the anterior of these is connected with the posterior division of the median vein by a short cross-vein, the median cubital. There is only one anal vein, which arises independently behind the cubital, and reaches the wing margin at the same point as the second division of the cubital vein.

The humeral and axillary cross-veins are well marked, the latter connecting the radial, median, and cubital veins, which are derived from the anterior trachea, with one another at the wing base. The radial median cross-vein connects the radial vein, just distal to its first division, with the anterior branch of the first division of the cubital vein. The median cross-vein forms the distal boundary of the discal cell, and the median cubital cross-vein connects the posterior division of the median vein with the anterior division of the cubital.

The cells will be recognized by the veins which form their anterior boundaries. The cell behind the fused second and third radial veins is the third radial cell, that behind the fifth, and limited above by the radial median cross-vein, the fifth radial cell. There are four median cells, the distal one of which is the first, while the second is divided into two parts by the median cross-vein. The anal cell corresponds to the anal lobe.

In the Muscoidean flies the venation is rendered simpler by the coalescence and suppression of many of the veins. Much importance is attached to the curvature of the fourth vein, which after a downward and outward course for the most part of its length turns upwards towards the apex of the wing, either terminating at the same point as the third vein, and thus closing the first posterior cell, or approaching very near it. It should be noted that in these flies the first longitudinal vein occupies a position corresponding to that in which the subcosta is found in *Haematopota*.

The Halteres

The *halteres*, or balancers (Plate XV, fig. 2) are characteristic of the Diptera, and are believed to be homologous with the metathoracic wings of other insects. They are small club-shaped bodies, situated behind the wings and behind and above the posterior spiracles of the thorax. Each arises from a small raised cushion, the rounded end being supported on a slender stalk. Both the raised base and the distal end are well supplied with nervous tissue, the cushion consisting mainly of a highly complex arrangement of sense organs. They are believed to function in regulating the flight and balance of the insect.

In the calypterate Diptera the halteres are covered by the squamae. Except for this they do not provide characters of use in classification.

THE LEGS

The legs are six-jointed, the joints being named from above downwards as follows:—coxa, trochanter, femur, tibia, tarsus and metatarsus. They are always fairly long, and may be, as in the mosquitoes, very long and slender. In the purely parasitic forms, such as *Hippobosca* and *Melophagus*, they are shorter but very stout. The relative proportions of the different joints does not vary much in the order. The *coxa*, by which the leg is articulated to the thorax, is short, generally oval in shape, and stout. The *trochanter* is a small joint which connects the coxa with the femur. The *femur* and *tibia* are long and generally cylindrical. The *tarsus* consists of five joints, of which the last four, the tarsus proper, are short, not much greater in length than in breadth; the first joint is often longer than the rest, and is sometimes called the metatarsus. As Colonel Alcock has pointed out, the use of the word metatarsus in this connection is hardly accurate, as the joint referred to is proximal to the tarsus, not distal to it.

The Legs (Plate XV, figs. 3, 5 and 7)

The joints of the legs may be coloured in various ways, and are frequently banded. They may have on them prominent spines or hairs, which may furnish characters useful in distinguishing species.

The foot of a fly consists of a pair of claws, with a pair of pads between them. The claws or ungues may be very delicate, as in the mosquitoes, or extremely strong and serrated, as in the Pupipara. They may be variously toothed and serrated, and thus yield useful distinguishing characters. All the claws may be alike, or those of the fore legs may differ from the other two pairs.

Between the claws there are other structures the form of which furnishes diagnostic features. These are the *pulvilli* and the *empodium*. The former are bilateral, and consist of small elongate pads of fine glandular hairs, which secrete a sticky substance, said to be used by the fly when crawling on a slippery surface. One of these pads arises near the base of each claw, and the empodium lies between them. Its form varies a good deal in the different families; it may consist of only a few moderately stout hairs, with a complex arrangement of nerve cells at its base, or it may consist of many hairs like those of the pulvilli, from which it is then not easy to distinguish ; in this case it is said to be pulvilliform. The pulvilli and empodium have some practical importance, for it is on them that bacteria may be carried from place to place by the fly.

THE ABDOMEN

The segmentation of the abdomen is much simpler than that of the other regions of the body, as each metamere is represented in the external wall by a pair of plates, the tergite and the sternite. These are transversely elongate, and in the unfed fly the tergite usually overlaps the sternite, thus concealing the membrane which unites them. Each plate overlaps the one behind it, and is attached to its neighbours by a narrow strip of membrane, which permits of movements of the segments on one another. The pleural membrane which connects the tergites and the sternites is lax enough to be capable of considerable distension when the fly is gorged with food. The number of segments visible externally varies from eight or nine to four, and progressively diminishes from the more primitive to the more complex forms, the diminution corresponding generally with a modification of the terminal segments into structures connected with the reproductive system. The terminal segments are always reduced in size. The opening of the alimentary canal is situated between the last tergite and sternite. In the higher forms, along with a reduction in the number of segments, there is also a great reduction in the extent of the sternites, which become restricted to a narrow space in the ventral middle line ; the tergites are increased in extent, but not sufficiently to compensate for the reduction of the sternites, so that there is a wide lateral area which is occupied by membrane. In the Pupipara the division of the abdominal wall into segments, and the separation between the tergites and sternites, are to a large extent lost, and the whole abdomen is enclosed by a tough but flexible integument. In these forms the anterior end of the abdomen is much contracted, and is joined to the thorax by a narrow 'waist'.

The External Genitalia (Plate XVIII)

The *external genitalia* consist of structures which are designed to assist in copulation, and, in the female, also in oviposition. They are formed from the terminal segments of the abdominal wall, and probably also from the remains of true abdominal appendages. It has long been recognized that these organs, especially those of the male, present an extraordinary degree of variability, and thus provide most useful distinctive characters by which forms very similar to one another may be distinguished. Unfortunately this variability makes them very difficult to study, and the homology of the parts has not yet been determined with any exactitude, a circumstance which rendrs the adoption of a satisfactory terminology very difficult. The same type of apparatus is found in each genus, however, and the parts have been successfully used, in the cases of *Phlebotomus* and *Glossina*, for the differentiation of species. It is evident that a classification founded on such definite morphological points is of much greater and more permanent value than one founded upon mere surface markings and colouration, which are not always constant for the species.

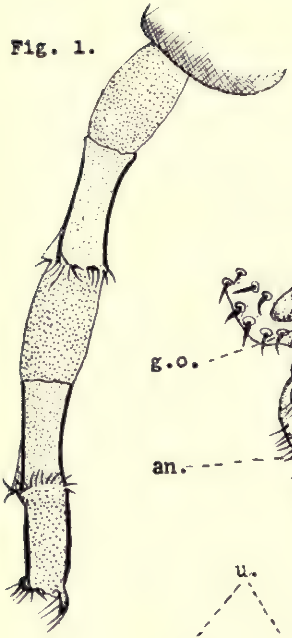
The male external genitalia are referred to under the general term *hypopygium*. They consist of a series of bilateral hooks or claws, with which the male attaches itself to the female during coitus, and a median set of structures which includes the penis and its sheath. Usually there are two pairs of claw-like structures, which may be either concealed within the abdomen when not in use or remain permanently outside; these are termed the *claspers*. One pair of them, usually the superior, is much larger than the other. The internal structures lie between the claspers, and are provided with a muscular mechanism by means of which the penis can be protruded at will through its sheath; the penis is connected with the seminal vescicles by an ejaculatory duct.

External Genitalia of Phlebotomus

The external genitalia of the male *Phlebotomus* (Plate XVIII, fig. 4) have been described by Newstead and by Annandale. They consist of two pairs of claspers, a sub-median lamella, certain intermediate appendages, and an intromittent organ. The *superior claspers* are dorsal in position, and form large and conspicuous objects at the end of the abdomen, thus affording a character by which the sexes can be distinguished at a glance. They are composed of two segments, which, in the position of rest, are acutely flexed on one another, so that the terminal one comes to lie in the vertical axis of the body. The proximal segment is larger and stouter than the distal; both are covered with a dense coating of hairs, and the terminal segment is provided with a series of large spines at the apex, to which Newstead attaches a specific value. The *inferior claspers* are smaller, and are unsegmented; they are placed ventrally and oppose the superior claspers, reaching as far as or beyond the distal end of the first joint of the latter. They may bear spines at the distal end. The *sub-median lamellae* are thin leaf-like structures, which lie between the inferior claspers, and are therefore only seen

PLATE. XVIII.

Fig. 1.



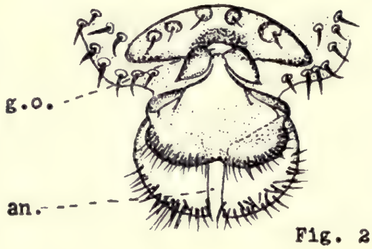
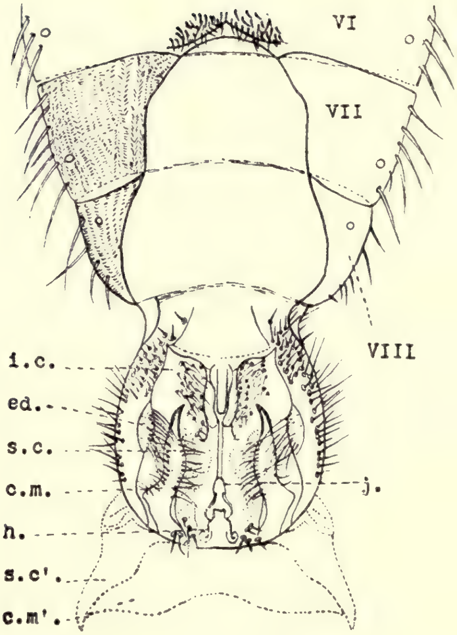


Fig. 2.


VI
VII
VIII
i.c.
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j.
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Fig. 3.

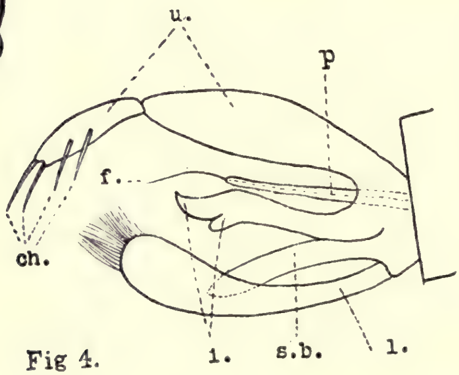
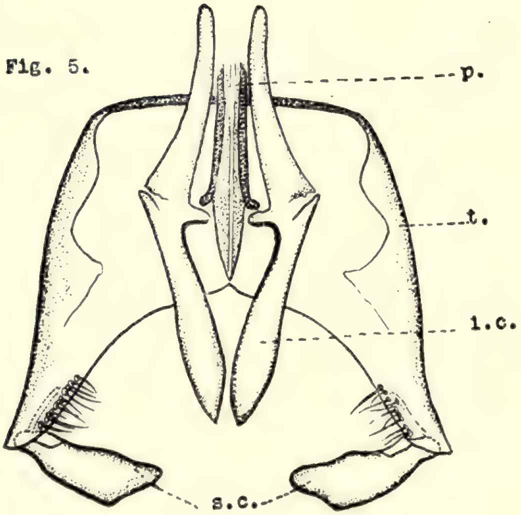


Fig 4.

Fig. 7.

Fig. 5.



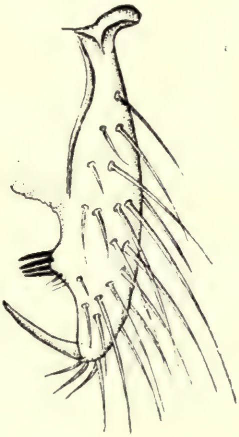


Fig. 6.

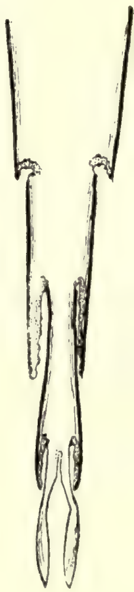


PLATE XVIII

Figure 1. The ovipositor of *Musca nebulo*, extended. × 22.

Figure 2. The distal end of the abdomen of *Hippobosca maculata*, ♀. g.o., the genital opening. an., the anal plates, one on each side of the anal opening. × 40.

Figure 3. The genital armature of *Glossina*, ♂, the hypopygium being extended backwards to display it. i.c., inferior clasper. ed., editum. s.c., superior clasper. c.m., connecting membrane. h., harpes. sc′., c.m′.; the dotted lines indicate the position to which the claspers and the membrane can be displaced. After Newstead.

Figure 4. Diagram of the external genitalia of *Phlebotomus*, ♂, after Annandale. u., upper or superior appendage. ch., chaetae. f., genital filament. i., intermediate appendage. p., intromittent organ. s.b., subgenital lamella. l., lower or inferior appendage.

Figure 5. The genital armature of *Tabanus albimedius*, ♂. s.c., superior claspers. i.c., inferior claspers. t., tergite of the last segment of the abdomen. p., penis, in its sheath. × 80.

Figure 6. One of the superior claspers of *Culex concolor*. × 100.

Figure 7. The terminal segments of the abdomen of a *Joblotia sp.*, ♀, forming a simple ovipositor. Note the loose membrane between the plates. × 60.

when the specimen is mounted dorsum uppermost. The *intermediate appendages* arise from the base of the first joint of the superior clasper, and occupy a median position, surrounding the penis. The *intromittent organ* is the central part of the whole apparatus, and contains the duct from the internal reproductive organs. It is a thin rod-like structure, highly chitinized, and has at the upper end a small oval chitinous swelling, at the lower end of which it receives the ejaculatory duct; at the distal end it terminates in a barbed chitinous penis. The swelling at the upper end of this organ contains much delicate muscle fibre, and is said to function as a pump to regulate the exit of the spermatozoa.

In the Orthorraphic flies it is usual to find the external genitalia strictly external, and some parts of them, usually the superior claspers, visible without dissection, as in *Phlebotomus.* In the Culicidae the superior claspers (Plate XVIII, fig. 6) are easily seen in mounted preparations, and their shape and the angle at which they are attached to the abdomen are used as characters in classification. In *Tipula* and *Asilus* the male genital armature is very conspicuous, and also of a very complex description. In *Tabanus* (Plate XVIII, fig. 5) the claspers are withdrawn beneath the terminal tergite, and can only be seen when dissected out. In the Cyclorraphic flies the parts are always concealed within the end of the abdomen, and can only be examined in specially made preparations. In *Musca* and its near allies the parts usually have a sinistral asymetry, and are composed of a complex of chitinous plates which have been differentiated as tergites and sternites of suppressed segments of the abdominal wall. The complexity of the parts is so great that it would serve no purpose to give a detailed description of them here. Those of *Glossina*, however, are of importance in classification, and demand further consideration.

External Genitalia of Glossina

The ventral aspect of the end of the abdomen in *Glossina* has on it a convex oval swelling, with a groove down the middle line. When the part is cleared in potash and dissected, it is found that the area of this swelling is formed by a separate plate of chitin, which is articulated by its posterior end to the ventral plate of the eighth segment of the abdomen, and is free for the rest of its periphery, so that it can be folded downwards and backwards until it projects at the distal end of the fly. The hypopygium as seen externally is in fact only the outer casing, the functional parts being concealed on its internal surface, and only displayed when the plate is everted. They consist of the following parts:—superior and inferior claspers, the editum, harpes, juxta, penis, a median process and a connecting membrane. The *superior claspers* are the largest and most important parts of the apparatus; they are stout hook-shaped organs, terminating in blunt chitinous points, which in many species are bifid. They are attached by their stout bases to that portion of the basal plate which is anterior when the hypopygium is closed and posterior when it is open, and are also capable of a limited amount of movement on their own attachments. The *editum* is a flange-like expansion, arising from the basal plate about the middle of its length on each side, external to the superior claspers. It bears a tuft of hairs. The *inferior claspers* are smaller than the superior, and are attached to the basal plate between them near the articulation with the eighth segment; they are softer, and do not terminate in chitinous points, but bear numerous fine and long hairs. Newstead attaches great importance to these organs, which appear to vary a great deal in the different groups of species. The *harpes* are bilateral organs situated between the attached bases of the superior claspers, and are most conspicuous in the *fusca* group. They may be armed with small chitinous hook-shaped sclerites near the terminal end. The *juxta* or *penis sheath* is a median structure extending from the apices of the inferior claspers to the level of the bases of the superior ones; it is tubular, divided and expanded at its distal end, and is, with the penis, everted along with the harpes. It has on each side a membraneous expansion, the *vesica*, supported by the harpes. The *median process*, when present, lies between the inferior claspers in the middle line, and is highly chitinized. The *connecting membrane*, present only in the *palpalis* and *morsitans* group, stretches between the superior claspers.

The modifications of this highly complex apparatus will be dealt with in a later chapter, in connection with the species for the differentiation of which the characters which it provides are used. The structures in *Glossina*, elaborate as they are, are not more so than in other groups, and the great difficulty in determining the relationships and homology of the parts must necessarily militate against their general use, for the present at least, in systematic Dipterology.

External Genitalia of the Female

The external genital apparatus of the female is generally much simpler than that of the male, and consists of a tube which can, to a greater or less extent, be protruded from the abdomen and again closed up like a telescope. It is only developed to a high degree in those forms in which the abdomen is shortened, as in the Muscidae, and reaches its highest development in those flies, such as *Musca*, which deposit their eggs in a soft substance. In the Orthorraphic flies it consists merely of some small plates of chitin, representing tergites and sternites of suppressed segments, which are connected together by membrane, and, in the resting condition, folded beneath the last visible segment of the abdominal wall. In the Culicidae an ovipositor as such can hardly be said to exist, but the terminal segments, much reduced in size, are closely compressed and at the same time connected together by a membrane loose enough to allow the plates to be extended on one another when the eggs are being laid. In *Tabanus* (Plate XIV, fig. 4) there are several suppressed plates under cover of the last segment, which are similarly attached, and can be drawn out by dissection, disclosing a simple ovipositor. The dorsal wall of this is formed by one broad plate, the tergite of the eighth segment, two small lateral plates which represent the tergites of the ninth and tenth segments divided into two lateral halves, and two anal plates, which project at the end of the abdomen, and represent the tergite of the eleventh segment similary divided in the middle line. The ventral wall is formed by a single plate of an irregularly quadrilateral shape, which may represent the sternites of the corresponding segments fused together. The greater flexibility of the dorsal wall allows the ovipositor to be bent downwards when it is in use.

Ovipositor of Musca

In *Musca* and those of its allies with similar breeding habits the ovipositor, when extended for use, is a tube equal in length to the rest of the abdomen, and of a diameter suitable for the accommodation of the egg. The membrane between the segments is so much increased that the tube when fully stretched owes at least half its length to the inter-segmental membrane, and the segments themselves are membraneous except for the small sclerites in the dorsal and ventral walls which remain to represent the original tergites and sternites. The sixth, seventh and eighth segments can be distinguished, and at the terminal end there is a small pair of plates, one dorsal and one ventral, which correspond to the tergite and sternite of the suppressed ninth segment. When in repose each of these divisions of the tube fits inside the one anterior to it, and the whole organ is retracted within the abdomen. When in use it curves downwards and a little forwards under the abdomen of the fly, and is in many species actually thrust into the dung or other soft substance in which the fly is about to deposit its eggs.

In the Pupipara, which deposit their larvae on the ground, there is no longer any necessity for a long tube, and the external genitalia are reduced to a simple transverse or cresentic slit, separated from the anus, which is posterior to it, by a stout piece of chitin. On account of the large size of the larva at the time it is deposited the slit, known as the *vulva*, is structurally adapted to enable it to dilate at the moment of parturition, and is provided with powerful muscles for the purpose. Dilatation is accomplished by retraction of the posterior lip of the orifice, and by separation of the two lateral halves of the anterior lip, which is composed of two plates of chitin meeting in the middle line but not continuous with one another. (Plate XVIII, fig. 2.)

The genitalia of the female flies do not provide characters used in classification.

CHAETOTAXY (PLATE XIX)

The value of the number and arrangement of the macrochaetae on the exo-skeleton as characters for systematic work was first recognized by Osten Sacken, and since the publication of his papers chaetotaxy has been a prominent feature in all descriptions of the higher Diptera. The subject is rather a difficult one, as it is often a very nice point to decide as to whether a particular hair shall be termed a macrochaeta or not, and on which of the more or less arbitrary regions of the thorax it is situated. As has been stated elsewhere, the reader will do well to seek the advice of an expert in the determination of species in such a difficult group of flies as the Muscoidea, in which the chaetotaxy is extensively used. The following account will suffice to give some idea of the subject, and to enable the student in most cases to separate the different genera. The distinction between many species in this group depends on such fine points that an actual comparison of the specimen with the type or a co-type is frequently necessary in order to identify it.

The bristles are named according to the situations in which they occur, the terms used being mainly those which have already been enumerated in connection with the structure of the exoskeleton.

On the head:—Commencing from the front, the *vibrissae* are a pair of stout and prominent bristles situated one on each of the prominent anterior lateral angles of the epistomal orifice, called variously the 'oral margin' or 'buccal orifice'. The *epistomal bristles* are situated

PLATE. XIX.

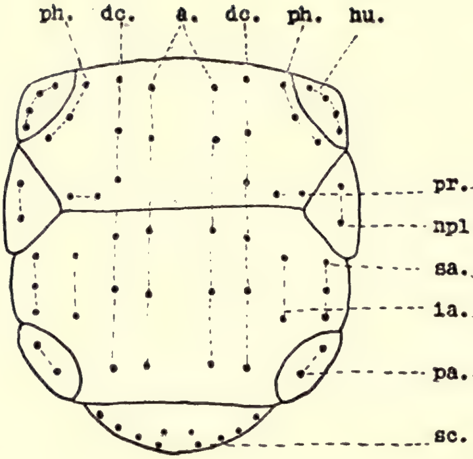

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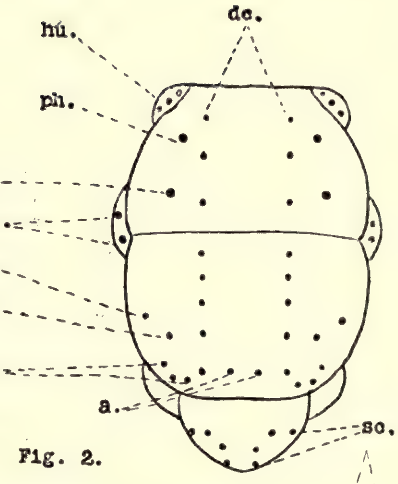
Fig. 1.



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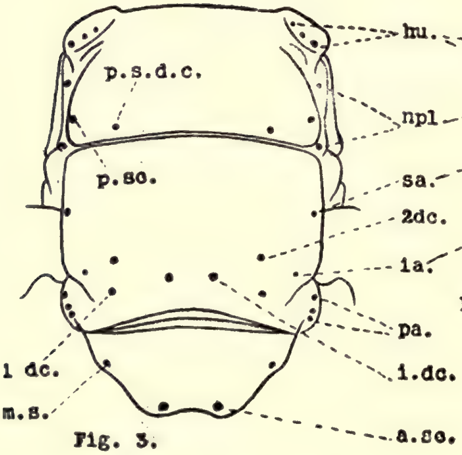
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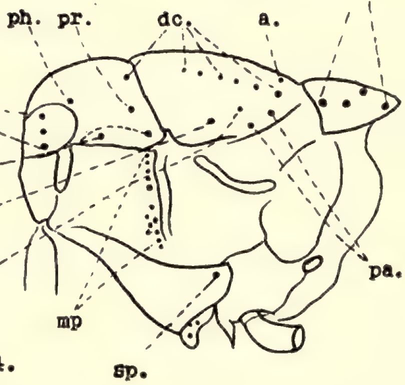
Fig. 3.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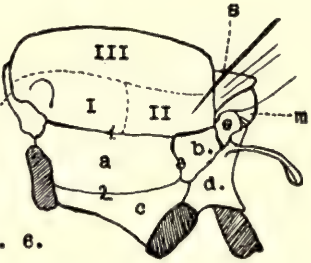
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Fig. 6.

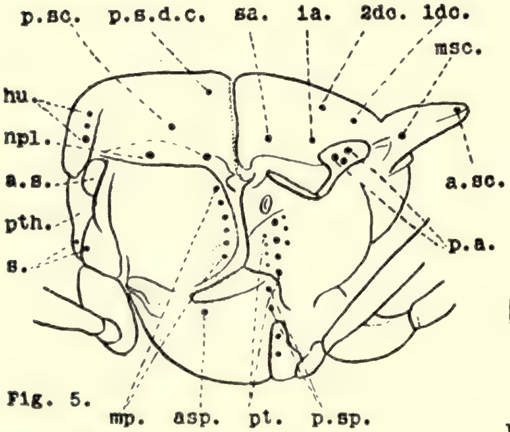
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Fig. 5.

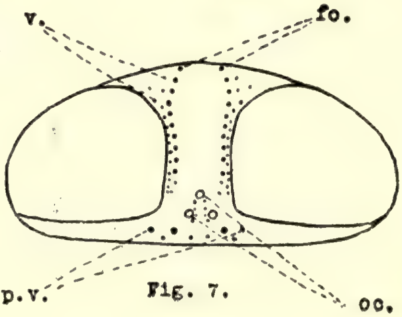

Fig. 7.

PLATE XIX

Chaetotaxy

Figure 1. Diagram showing the dorsal thoracic bristles, after Williston.

Figure 2. Thorax of *Musca domestica*, dorsal side.

Figure 3. Thorax of *Glossina palpalis*, dorsal side, after Austen.

Figure 4. Thorax of *Stomoxys calcitrans*, lateral aspect.

Figure 5. Thorax of *Glossina palpalis*, lateral aspect, after Austen.

Figure 6. Diagram of the parts of the thorax, after Mik, from Osten Sacken. p., pronotum. s., scutellum. m., metanotum. 1. dorsopleural suture. 2. sternopleural suture. 3. mesopleural suture. *a.*, mesopleura. *b.*, pteropleura. *c.*, sternopleura. *d.*, hypopleura. *e.*, metapleura. I. dorso-humeral region. II. dorsoalar region. III. dorso-central region.

Figure 7. Head of *Musca domestica*, seen from above.

Reference letters, figure 6 excepted.

a.	Acrostichal or inner dorsocentral bristles.
as.	Anterior spiracle.
acs.	Apical scutellar bristle.
asp.	Anterior sternopleural bristle.
dc.	Dorsocentral bristles.
1dc.	First dorsocentral bristle.
2dc.	Second dorsocentral bristle.
fo.	Fronto-orbital bristles.
hu.	Humeral bristles.
ia.	Intra-alar bristles.
mp.	Mesopleural bristles.
msc.	Marginal scutellar bristles.
npl.	Notopleural bristles.
oc.	Ocellar bristles.
pa.	Post-alar bristles.
ph.	Post-humeral bristles.
pr.	Prae-sutural bristles.
psp.	Posterior sternopleural bristles.
psdc.	Prae-sutural dorsocentral bristle.
psc.	Prae-sutural dorsocentral bristle.
pt.	Pteropleural bristles.
pv.	Post-vertical bristles.
sa.	Supra-alar bristles.
v.	Vertical bristles.

on the peristomalia, which are ridges on the lower edges of the peristoma, or the cheeks, regions which correspond to those described as the genae.

Cephalic Bristles (Plate XIX, fig. 7 & Plate III, fig. 1)

The *facial bristles*, often very conspicuous, are situated on the front of the head, external to the antennae, and above the vibrissae. The *lateral facial bristles*, when present, are external to them and on the lower part of the head. The *frontal bristles* are situated on the upper part of the head, external to the ptilinal suture, on each side of the insertion of the antennae, and above and external to the facial bristles; the rows of the two sides converge towards one another near the vertex of the head. There may be two pairs of *vertical bristles*, an inner and an outer, at the upper and inner angle of the eye, and there may be *post-vertical bristles* behind them. In front of the vertical bristles, and behind the frontal bristles, there are three sets of *fronto-orbital bristles*, upper, middle and lower, the last named being rarely present; the first are always reclinate, and may appear as a continuation of the frontal rows posteriorly; the second are always proclinate and are generally nearer the orbit. The *ocellar bristles* are situated in the ocellar triangle at the vertex of the head; *post-ocellar* and *prae-ocellar* bristles may be present. The *facio-orbital bristles* are situated, when present, on the narrow strip between the eye and the lower half of the ptilinial suture. There may also be bristles on the cheeks.

Thoracic Bristles (Plate XIX)

On the thorax :—*Humeral bristles* are situated on the humeral callus, and *post-humeral* ones on its inner margin. The *notopleural bristles*, usually two on each side, are situated on the edge of the praescutum near its posterior borders, that is to say, between the humerus and the root of the wing. The *prae-sutural* bristles are placed near the lateral borders of the praescutum, just in front of the suture between it and the scutum. On the scutum there are the *supra-alar* bristles, immediately above the root of the wing, usually three in number, and the *intra-alar*, internal to them. In the middle portion of the thorax there are two rows of bristles on each side, extending through the praescutum and the scutum. The inner two rows are termed the *acrostichal* bristles, the outer two the *dorsocentral*. The *post-alar* bristles lie behind the base of the wing, and behind and below the supra-alar. On the margin of the scutellum there is a row of *scutellar* bristles, and there may be also others removed from the margin. On the side of the thorax there are the *propleural*, immediately above the coxae of the forelegs; the *mesopleural*, on the mesopleura, near the angle between the dorsopleural and mesopleural sutures (or, using other terms, on the episternum of the mesothorax, near its upper and posterior angle) ; the *sternopleural*, on the mesosternum, below the suture between it and the episternum (mesopleura) ; *pteropleural*, rarely present ; *metapleural* or *trichostichal*, on the metapleura ; and *hypopleural*, usually small, on the hypopleura.

On the abdomen :—*Marginal* bristles, situated on the posterior margins of the tergites ; *discal*, on the tergites but removed from the margins ; and *lateral*, near the lateral margins of the segments.

The following terms are used to denote the inclination of the bristles or groups of bristles :—*erect*, *suberect*, *proclinate*, *reclinate*, *convergent*, *decussate*, or *cruriate*. The bristles themselves are described as *strong*, *weak*, represented by hairs, *hair-like*, or normal with hairs among the bristles. The arrangement of a group may be in a single row, in more than one row, *parallel*, *convergent*, or *divergent* ; they may be *apical*, as on the scutellum, or *sub-apical* ; arranged in pairs or singly. The actual number is always stated unless large.

The application of the above nomenclature requires a good deal of experience, and it is of great advantage to obtain a few named and described specimens, and to compare the chaetotaxy with the description of the fly by a recognized authority.

CHAPTER II

SECTION 2

THE INTERNAL ORGANS

THE MUSCLES

THE muscles serve to move the appendages on the body, and the joints of the appendages on one another; they also bring about movements of one segment on its neighbours, and of the separate plates of the exo-skeleton of each segment on one another, when these are not fused together. They always arise from the internal surface of the exo-skeleton, and the joint over which they act may be, as in the legs, a more or less definite articulation formed by a moulding of contiguous parts of the chitinous wall, or it may be merely a space in which the exo-skeleton is represented only by a flexible membrane, such as exists between the segments of the abdomen.

The peculiarities of the structure of insect muscle have been frequently described, and need not be dealt with here, as they do not concern the parasitologist. There is one physiological feature, however, which is of great importance in relation to the mechanism of feeding and of flight, namely, the capacity which insect muscle possesses for a very high degree of rapidity of contraction. It is stated by Marie that the wing of the fly can make 330 contractions per second, a rate which is probably not equalled by any other creatures, and it is this capacity which enables it, with a comparatively small wing area, to support a weight which must be relatively enormous. Similarly, it is the capacity of the muscles for rapid action which enables the mouth appendages of the blood-sucking forms, with a comparatively small armature and a limited excursion, to act as an extremely rapid and effective piercing apparatus.

Arrangement of Muscles

The muscles of the mouth appendages have already been sufficiently described in connection with the parts on which they act. The antennae and palps also possess small muscles, which are able to produce a limited amount of movement of the joints upon one another, and of the whole appendage upon the head. The muscles of the legs pass from above downwards, those of the first joints arising in the ventral part of the thorax from apodemes or chitinous protuberences, and passing into the tubular space enclosed by the integument of the leg. In the remaining joints the muscles arise above, and are inserted below, the articulation on which they act.

The muscles of the body wall are arranged primarily in two sets, acting, so far as the shape of the body is concerned, in opposition to one another. One set is more or less circular, and connects the separate plates of the segment in which it lies; by approximating them it reduces the transverse diameter of the body, with a corresponding increase in the long diameter. The other, which is internal to this, connects the segments with one another, running in an antero-posterior direction, so that its contraction diminishes the length of the body by approximating the segments. This primitive arrangement is altered in a characteristic manner in the three regions of the body.

In the head the exo-skeleton of all the segments has become welded to form a chitinous box, the walls of which permit of no movement. The muscles of the body wall have, therefore, disappeared altogether. There are a few small bundles in the lateral walls of the neck, which suffice to move the head on the thorax.

In the thorax the muscles are very greatly enlarged, and modified in their arrangement, in order to provide the motive power for flight, and it is on account of their large mass that the thorax in the Diptera is so conspicuous. They fill up almost the whole of the cavity, the various structures which pass through it being compressed into the ventral angle. (Plate XX, fig. 2.)

Flight

Flight is accomplished by rapidly repeated alterations in the vertical and longitudinal diameters of the thorax, which impart a vibratory movement to the wings, and since the wings of the Diptera are mesothoracic outgrowths, it is the muscles of the mesothoracic segment which have been specially developed. It was pointed out in connection with the anatomy of the thorax that this segment has become increased to such a disproportionate extent as to reduce the segments in front and behind to mere rings of chitin, and that it is separated from the metathorax by a diaphragm-like ingrowth, the mesophragma. It is in the space anterior to the mesophragma that the main mass of the muscle is contained, the muscles of the other two segments, except those of the legs, being reduced to very thin sheets. The muscles of the mesothorax consist of an external set which pass somewhat obliquely downwards and backwards from the dorsal to the ventral wall, and a longitudinal set, which pass from the anterior end of the thorax to the mesophragma, in the upper two-thirds or more of the cavity. It will be recalled that the dorsal and lateral walls of the mesothorax are not welded together by continuity of their chitin, but that there is a lateral area between them where the wall of the thorax is membraneous, thus permitting of some alteration in the shapes of the cavity; and that there is a separate mechanism, consisting of a set of chitinous rods arranged as a system of levers, by means of which the wing can be brought into position for flight.

Now when the wing is in position for flight, the veins project for a short distance within the cavity of the thorax, and are so arranged that the muscles act on them as on a lever, the longitudinal muscles, which increase the vertical diameter of the thorax, causing a downward displacement, and the antero-posterior set a corresponding upward displacement. If the wing surface presented a uniform resistance to the air throughout its area nothing would result from this, but this is not the case, for the veins of the wing are always stronger in its anterior portion, and this part consequently yields less to the pressure than the part behind it. In this way the surface becomes an inclined one, and the vibratory movement is therefore accompanied by translation. The mode of propulsion through the air has been aptly compared by Marie to that by which a boat is moved through the water by a waterman's scull.

It is evident that, within certain limits, the more the anterior veins are strengthened and the posterior ones reduced the more effective will the blade-like action of the wing become, and we have here a confirmation of the dictum of Williston, that flies with such a venation are more highly organized and more recent than those in which the wing veins are distributed evenly over the surface. We may contrast the two extremes of *Phlebotomus* and *Hippobosca*, the former of which, notwithstanding its large wing area in proportion to the body weight, is a feeble flier, while the latter, even when it contains a full grown larva, is extremely active when on the wing.

In the abdomen the arrangement of the muscles is simpler, and corresponds with the more primitive structure of the body wall. The vertical muscles are only feebly developed, and connect the tergite and sternite of each segment with one another, the longitudinal muscles connecting adjacent terga and sterna in a similar manner. The two sets move the abdominal segments on one another, and can flex the abdomen downwards, as in oviposition. Possibly they also assist, after the manner of the abdominal muscles in mammals, in the expulsion of the ova. They also provide the motive force for respiration.

THE RESPIRATORY SYSTEM (PLATE XX)

In insects respiration is carried on by a system of tubes which has many analogies with the arterial system of vertebrates. The tubes open on the surface of the body, and are there in communication with the external air. As they pass inwards they divide into innumerable branches, which, progressively diminishing in size, conduct the air into the innermost interstices of the tissues for the supply of the body cells. Those tissues in which the metabolism is the most active, as for instance the mid-gut, in which digestion takes place, and the ovaries, receive the largest supply of air.

Spiracles

The external openings through which the air enters the tracheae or air tubes are termed the *spiracles* or *stigmata*. Normally one would expect to find one pair to each segment, and this arrangement is, in fact, for the most part preserved, but some have been suppressed on account of the shortening of the body. In the head, in which no respiratory movements can take place, there are no spiracles, nor are there any in the very much reduced prothorax. The meso-and meta-thoracic segments have always a pair each, that of the former being the largest in the body. In the abdomen the anterior segments have a pair each, but the reduced segments at the posterior end, and those segments which are modified to form the external genitalia, are without them. The number of abdominal spiracles is naturally less in the Cyclorrapha than in the Orthorrapha, and the size of the tracheae from the thoracic spiracles is increased to a commensurate extent.

The situation of the thoracic spiracles differs a little in the two divisions of the Diptera. In the Orthorrapha, in which there is a distinct membraneous interval between the dorsal and lateral walls, the anterior spiracle is usually situated at the anterior end of this interval and is separated from the chitinous portion of the thoracic wall. The posterior or meta-thoracic spiracle is placed in a similar membraneous area between the lateral plates of the mesothorax and metathorax. In the Cyclorrapha, in which the consolidation of the thorax has proceeded further with the development of a more powerful and rapid flight, the membraneous areas are much reduced, and the spiracles are displaced so as to lie between contiguous lateral plates, to which they are closely connected by strong bars of chitin. Each spiracle is an oval or dumb-bell shaped opening, the margin of which is maintained by a rim of chitin, more or less thick in accordance with the density of the rest of the thoracic wall. The opening is guarded by a series of teeth of various forms, designed to prevent the ingress of solid particles; they may be simple and comb-like, or extremely minute, thin, and numerous, arising from a large number of short common trunks and bending in all directions across the opening like the branches of a tree. (Plate XX, fig. 5.) Posterior to the opening there is a small vestibule, provided with a simple valve and muscle, by means of which the size of the inlet can be regulated.

The abdominal spiracles lie in the membrane between the sternites and tergites. Each is placed a little anterior to the segment to which it properly belongs, and the number is usually less than the number of visible segments. The first pair lie close to the distal end of the metathorax. They resemble the thoracic spiracles in structure, but are generally smaller. The abdominal spiracles do not, however, diminish progressively in size as one might expect, the largest being usually that which admits the air destined for the supply of the ovaries.

Arrangement of Tracheae

In a primitive arrangement of the parts each pair of spiracles would give rise to a pair of branching tracheal tubes for the supply of the segment, but in the complex imago of the Diptera there is a considerable deviation from this type, due partly to the suppression of some spiracles and their tracheae, and partly to the dislocation of others from their segments in a forward direction. The system is rendered more complex by the anastomosis of the branches of one tracheae with those of its fellow of the opposite side and with those of the adjacent segments; the anastomosis takes place, not between the ultimate divisions, but between tracheae of considerable size. In the main features, however, the segmental arrangement is preserved, and most of the branches from a spiracle go to supply the tissues of the segment to which it belongs.

The distribution of the main branches will be understood sufficiently well from the figures given. (Plate XX.) The head receives its supply from the anterior or mesothoracic spiracles by means of a pair of tracheae which pass through the neck. The two thoracic spiracles supply the huge mass of muscle contained within the thoracic cavity, and also the legs; some branches from the posterior spiracle pass into the abdomen and anastomose with the abdominal tracheae. Each abdominal spiracle gives rise to a short trunk, which divides almost at once into a number of branches, some of which break up for the supply of the adjacent viscera and the body wall, while others pass backwards and forwards to anastomose with the tracheae from the adjacent spiracles. One branch passes straight across the body immediately below the dorsal plates, there anastomosing with its fellow of the opposite side to form a loop below the heart.

Air Sacs

In the great majority of the air tubes, at least in the Orthorrapha, the diameter is uniform, and is reduced in a simple manner at each bifurcation, but in certain parts there are dilatations, in which, as will be seen presently, the specialized structure of the wall of the tube is not found. In *Tabanus* there are two of these air sacs in the anterior end of the abdomen, which, on account of their white colour and large size are very conspicuous when the abdomen is opened without damaging them. They always contain air, but are not distended to such a degree as to make their walls taut. The tracheae of the head have always a large number of air sacs on them, especially in the region of the brain, and these have an important function in relation to the mechanism of feeding, as already described. In the Cyclorraphic flies (Plate XX, fig. 6) almost all the main branches of the thoracic tracheae are dilated to form sausage-shaped sacs, from which small tracheae are given off, these breaking up at once into a large number of branches for the supply of the adjacent tissues. One of the branches from the anterior spiracle on each side passes into the abdomen, and there dilates into a large sac, which occupies a considerable proportion of the abdominal space. (Plate XX, fig. 6.)

Structure of Tracheae

The structure of the tracheae and air sacs will be best understood by a reference to their mode of origin. They represent invaginations of the ectoderm, and as such are lined, from the spiracle to the final divisions, with chitin which is continuous with that of the exo-skeleton. Their outer surfaces, that is, those which are in contact with the body contents, are lined by a layer of cells which is continuous with the hypodermis or chitinogenous layer of the exo-skeleton. The internal lamina consists of a very thin but uninterrupted layer of chitin, but in all except the most minute tracheae this is modified in a remarkable manner to form the well-known *spiral thread.* (Plate XX, fig. 4.) When examined under a high magnification, and preferably after some preliminary maceration in potash, the wall of the tube is seen to be traversed by a large number of extremely thin annular threads, which pass four or more times round

PLATE XX

Figure 1. The respiratory system of *Culex*. c.tr., cervical trachea. a.s., anterior spiracle, with its large trachea. p.s., posterior spiracle. d.a., dorsal arch, running below the heart. l.tr., lateral trachea. a.tr., trachea anastamosing with one from the next spiracle: similarly in the other segments. The abdominal spiracles are numbered in order.

Figure 2. A section through the thorax of *Haematopota*, to show the muscles. l.m., the longitudinal muscles. v.m., the vertical muscles. tr., trachea. d.c., the duct of the crop. sl.g., the salivary glands. pv., proventriculus. n., nerve cord. Note the membraneous area in the lateral wall. × 45 about.

Figure 3. Respiratory system of *Tabanus*. br., brain. a.s., air sacs. ab.s., first abdominal air sac. ab.s′., second abdominal air sac. Other letters as in Figure 1.

Figure 4. A trachea, highly magnified, to show the spiral thread, and the nuclei of the hypodermal cells which lie on the visceral surface.

Figure 5. The anterior thoracic spiracle of *Musca*, to show the fine arborescent filaments of chitin which guard the entrance to the trachea. × 440.

Figure 6. The tracheal sacs supplied by the anterior thoracic spiracle (a. th.). In this figure the tracheal sacs supplied by the posterior thoracic spiracle and the sterno-dorsales muscles of the left side have been removed. The first abdominal segment has been removed to show the large abdominal air sacs (ab. s.) and an abdominal trachea which is supplied by the second abdominal spiracle (a. sp.). After Gordon Hewitt. A. c. s., anterior cephalic sac. a.v.s., anterior ventral thoracic sac. c.tr., cervical tracheal duct. d.c., dorsal cephalic sac. do., dorsales muscles. H., haustellum. l.tr.s., longitudinal tracheal sac. p.c.s., posterior cephalic tracheal sacs. p.v.s., posterior ventral thoracic sac. p.op. periopticon. Ros., Rostrum. v.c.s., ventral cephalic sac.

PLATE.XX.

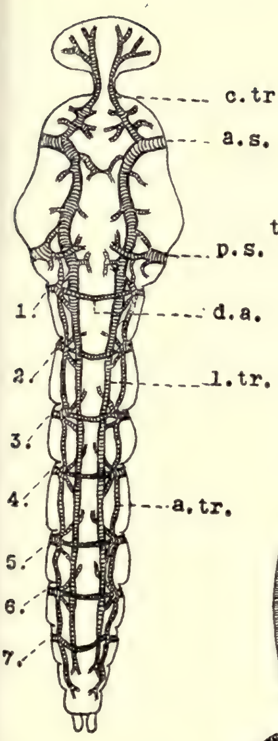
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Fig. 1.

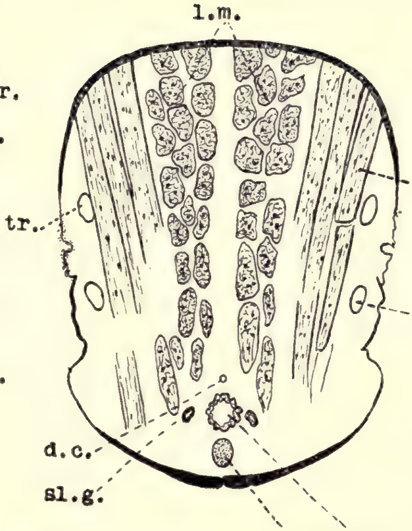
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Fig. 2.

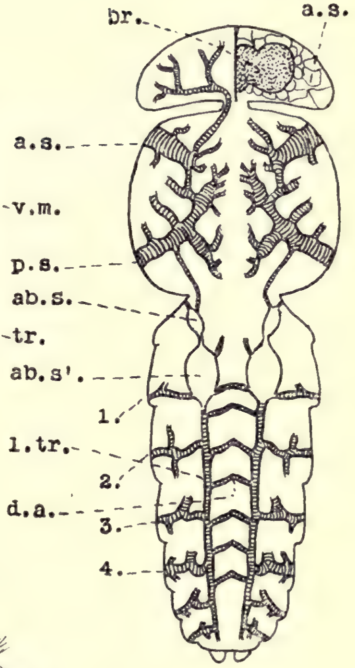
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Fig. 3.

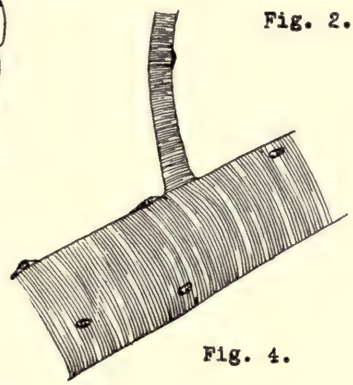


Fig. 4.

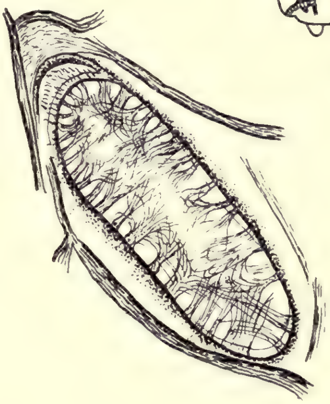
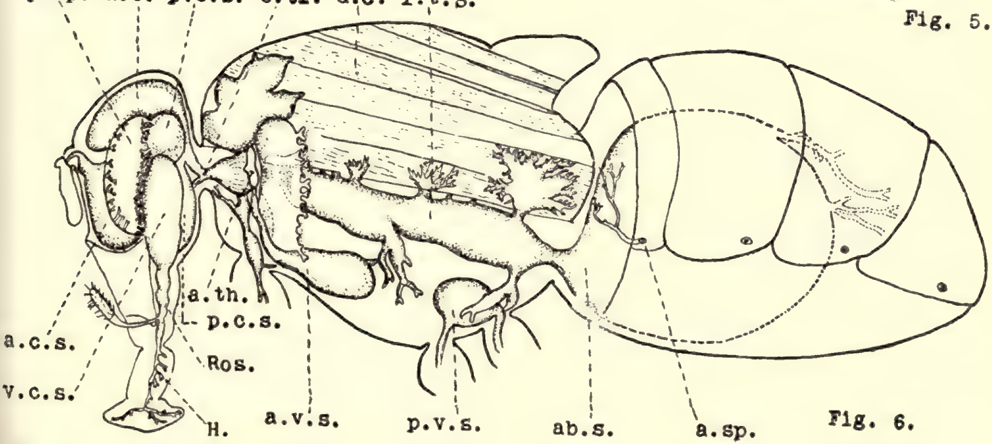


Fig. 5.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d.c.
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p.c.s.
a.c.s.
Ros.
v.c.s.
H.
a.v.s.
p.v.s.
ab.s.
a.sp.

Fig. 6.

the lumen in a corkscrew-like manner, the turns being so closely compressed together that they appear to be transverse. Where each length of thread ceases there is a short interval, after which another arises; the threads never pass into the branches, nor do they ever bifurcate. When seen in sections of the larger tracheae the thread projects a little into the lumen, giving it a ridged appearance. The intervals between the turns of the thread are filled in by a very thin layer of chitin.

The arrangement of circular or spiral thickenings in the wall of a thin chitinous tube is one admirably adapted to ensure that the lumen of the tube will be kept open even if the angle at which it is flexed becomes greatly altered; in other words, to prevent occlusion by kinking. Such occlusion might readily occur in the tracheae during the movements of the body, or when the mid-gut or crop is distended with blood.

The outer or hypodermal lamina of the tracheal wall, which is in contact with the internal organs, is very thin, and is only recognized by the scattered nuclei which lie on the surface of the tubes. It is continued to the most minute branches of the tube, after the spiral thread has ceased, and as it reaches to the intercellular spaces while still in continuity with the hypodermis, it forms a sort of peritoneum, within which the internal organs are contained.

The structure of the air sacs is essentially the same as that of the tracheae. There is, however, no spiral thread, and the layer of chitin may be greatly thickened. In the sacs of the head, and to a lesser extent those of the thorax in the more specialized flies, the wall is very dense and tough, and, as it is often adherent to surrounding tissues, the sacs are in some cases extremely difficult to dissect away from the soft parts. The sacs in the abdomen are as a rule very thin-walled, and have a dead white colour and a peculiar waxy appearance. When ruptured in saline solution the wall of the sac spreads out just as do very thin paraffin sections.

In addition to their function of conveying air to the tissues the tracheae are put to another use, in that they serve to support the internal organs and to retain them in position. Their flexibility enables them to adapt their position to that of an organ of changing dimensions, such as the mid-gut.

Respiration

The movements of respiration in insects depend on the contraction of the longitudinal and vertical muscles, and are mainly restricted to the abdomen when the fly is in the resting position. The exact mechanism is not clearly understood, but it is probable that the total capacity of the body cavity is diminished by the contractions of these muscles, with the result that the air is expelled; inspiration is accomplished by the elastic recoil of the spiral thread, which restores the trachea to its original form. The air sacs would appear to play an important part in this mechanism.

The chitinous nature of the wall of the tracheae and air sacs is of the greatest importance from the point of view of technique. Ordinary fixatives will not penetrate through chitin, and, even if the fluid were to find its way through the spiracles, it is still shut off from the soft tissues.

THE ALIMENTARY CANAL

The alimentary canal in its simplest form is a straight tube commencing at the mouth and running backwards through the body to terminate at the anus, which is situated at the extreme posterior end of the abdomen. Some parts of this are specialized for one function and some for another, and in most Diptera the tube has outgrown the body cavity in which it lies, and has become twisted and coiled upon itself. It is held in position by the tracheae which supply it with air, and lies in the median position, that is, below the dorsal vessel and above the ventral nerve chain.

A proper conception of the morphology of the alimentary tract can only be obtained by reference to its mode of origin. In the developing embryo insect the tract consists of three parts, which arise in different ways. At each end of the embryo there is an invagination of the cuticle, which proceeds until two deep pits are formed; that at the anterior end is termed the *stomodaeum*, and that at the posterior end the *proctodaeum* (Plate I, fig. 3). Between them a cleavage occurs in the mesoblast, and this develops into a cavity, which in time becomes continuous with the stomodaeum and the proctodaeum, so that a complete canal is formed opening at the anterior and posterior ends of the body. The distinction between these three parts influences both their structure and their function, and should always be borne in mind. The invaginations of the cuticle are lined with a chitinous layer which is continuous with the integument, and can take no part in the actual processes of digestion, whereas the middle portion, or mesenteron, has no such layer, and is the true stomach or digestive chamber. It is lined with a specialized epithelium, and may be otherwise modified in connection with the digestive process.

Development

Divisions

The alimentary tract in the adult insect is divided into a number of parts, each of which is more or less specialized for a particular function. The arrangement in the Diptera does not differ much from what is found in other insects, except in the details of structure, and the homology of the parts is as a rule easily made out. The parts may be enumerated as follows:—

Developed from the Stomodaeum.	The Buccal cavity, with the epipharynx and hypopharynx. The Pharynx. The Oesophagus. The Crop, or food reservoir. The Proventriculus, homologous with the gizzard of insects which take solid food.
Developed from the Mesenteron.	The Mid-gut.
Developed from the Proctodaeum.	The Intestine, or Hind-gut, which may be divided into a proximal part, the Ileum, and a distal part, the Colon. The Rectum.

The three divisions are also known as the fore-gut, mid-gut and hind-gut respectively. It should be noted that these terms have a definite morphological significance, and are not to be used merely with reference to position. In the Muscid flies the term 'Intestine' is applied to a part of the mesenteron; confusion will not arise if the position of the Malpighian tubes is kept in mind.

In addition, there are two sets of structures accessory to the alimentary tract, namely, the salivary glands, connected with the stomodaeum, and the Malpighian or urinary tubules, inserted into the proctodaeum.

All the above parts can be distinguished in the Diptera. As regards the length of the canal, there is a progressive increase, and a tendency to the formation of a tube with a uniform diameter throughout, as one passes from the simpler Orthorrapha to the Cyclorrapha, and at the same time an increase in the length of the salivary glands. In the Culicinae the alimentary tract when drawn out is only a little longer than the body of the fly, while that of *Musca* is three or more time the length.

The *buccal cavity* and the *pharynx* have already been described in connection with the mouth parts. Together they form the sucking apparatus by which the food is drawn from the wound up the canal in the proboscis and passed on to the oesophagus.

The *oesophagus* is a simple tube, which connects the pharynx in the head with the proventriculus in the thorax. Immediately after it leaves the pharynx it passes backwards through the brain, and after reaching the thorax it divides into two branches of about equal size ; one of these passes into the proventriculus, while the other is continued onwards through the thorax as the duct of the *crop* or food reservoir. The latter is a thin-walled sac, capable of considerable distension, situated in the abdomen. The *proventriculus*, when present, lies either in the posterior end of the thorax or at the anterior end of the abdomen, and often has a considerable amount of muscle in its wall. It is the homologue of the gizzard of other insects, but as the Diptera have no solid food to grind it has no internal teeth, and appears in many forms to function as a valve. The *mid-gut* is the main digestive part of the alimentary tract, and is lined by a columnar secreting epithelium. It is capable of great distension in some forms. The separation between the mid-gut and the *hind-gut*, in the less specialized forms at least, is marked by the insertion of the Malpighian tubes into the wall of the canal. Posterior to the mid-gut the canal may be coiled and twisted to a considerable extent, owing to the disproportion in length between it and the cavity in which it lies. The upper part is generally the narrowest, and may for the sake of convenience be termed the ileum, the lower and wider portion being known as the colon, though it is important to note that these are mere terms of convenience, having no definite morphological significance, and cannot be applied in all cases. In the Muscid flies other terms are in common use to distinguish the different regions. The last portion of the canal is dilated to form a pear-shaped *rectum*, in which there are certain curious trumpet-shaped bodies called the *rectal glands* or *rectal papillae*.

There is a good deal of variation in the shape and structure of the alimentary canal in the two main divisions of the Diptera, and it will be convenient to treat them, to a certain extent, separately. The modifications found in the higher forms are due mainly to the increased length of the canal, and to its more uniform calibre.

Tabanus will again serve as an example, as it is fairly easy to obtain and has a simple alimentary tract (Plate XXI).

The *oesophagus* commences at the posterior end of the pharynx, and at once narrows down to a thin tube. It first passes straight backward through the middle of the brain, emerging at its lower border. It then passes through the neck, lying at first between the two main nerve trunks which pass from the brain to the thorax, and later upon the single trunk formed by the fusion of these, a point which is well demonstrated in serial sections. After entering the thorax it divides almost at once into two branches, one dorsal to the other, the dorsal branch being in the same line with the cervical portion of the oesophagus. The two branches are equal in calibre, but differ greatly in length. The dorsal one runs straight through the thorax as the *duct of the crop*, while the ventral one terminates after a very short course by entering the proventriculus just behind its anterior end. The oesophagus, in fact, appears to end undivided in the dorsal surface of the proventriculus, and the duct of the crop to leave it at the same point. The two openings are situated on a slight elevation in the dorsal wall of the proventriculus.

Alimentary Tract of Tabanus.—Oesophagus

At the commencement of the oesophagus no cellular lining can be distinguished, and the wall appears to consist only of an unstainable chitinous membrane, but as the tube leaves the brain it comes to have a layer of thin and flattened cells underneath the chitin. As the tube passes through the neck the cells become more numerous and more regularly arranged, until there is a regular layer of squat cubical cells, set on a distinct basement membrane, while the chitinous intima is at the same time reduced in thickness. The basement membrane of the cells, which are, of course, hypodermal in origin, is of considerable thickness.

The duct of the crop is precisely similar to the thoracic portion of the oesophagus, except that its lumen is a little narrower.

The *crop* is a small bi-lobed sac with an extremely thin wall. This is composed of a single layer of very small flattened cells, external to which there are many small muscle fibres arranged in an irregular network. From what has been said with regard to the relations of the two divisions of the oesophagus it will be evident that the crop is in a direct line with the posterior end of the pharynx in the head.

Crop

The function of this sac is a little difficult to determine. It often contains a few small bubbles of gas, and is as frequently empty and collapsed, when it assumes the shape shown in the figure. (Plate XXI, fig. 1.) The present writers, in the course of several hundred dissections, have never found it to contain fresh blood even in flies killed while in the act of feeding, though on rare occasions a little pigment, presumably derived from blood, has been seen in it. In freshly-killed flies, taken in the act of feeding and with the mid-gut filled with blood; its walls can often be seen to contract in a peristaltic manner, such as would result in expelling its contents. The view most consistent with the anatomical appearances is that it acts as a primary receptacle for the blood, which is passed into it direct from the pharynx as it is sucked up, and is passed on into the mid-gut by the contraction of the walls of the sac. The presence of the blood in the sac acts as a stimulus to provoke its contraction, so that the blood never remains in it, but is returned up the duct as fast as it is received. This is all the more likely to be the case in that the duct of the crop is in line with the pharynx, while the part of the oesophagus leading to the proventriculus is bent at an angle. The straight course for the blood is into the crop.

The term ' sucking stomach ', frequently applied to this structure both in this and in other flies is a misnomer, for whatever its function may be it certainly does nothing to assist in sucking up the blood, neither is it a stomach, in the sense of having any digestive action. The term oesophageal diverticulum is also undesirable, as hiding the essential similarity of this structure with that in other insects.

Proventriculus

The *proventriculus* is a long flattened tube, extending from the thoracic inlet to the commencement of the abdomen. In its anterior two-thirds it is about twice as broad in the transverse diameter as it is in the vertical, so that its lumen is a transverse slit, but posterior to this it becomes rounder, with a small circular lumen, and also much narrower. At the anterior end there are two broad lateral expansions, the anterior and external angles of which project forwards and receive minute nerves from the head. This part, when seen from the dorsal aspect, resembles a butterfly with expanded wings. With the exception of the posterior and rounded part the whole of the surface of the organ is studded with small regularly arranged elevations, which give it a mammilated appearance when examined under a low power; there are four rows of such elevations on each of the dorsal and ventral surfaces, and two rows on each lateral border.

The opening by which the oesophagus communicates with the proventriculus is situated in a small elevation on the dorsal surface, not at the extreme end, but a little behind it.

The minute structure of the wall of the proventriculus is essentially the same as that of the oesophagus, but the appearance on section is profoundly modified by the great increase in the thickness of the wall and the bunching up of the cells to form the elevations referred to above. A section through the middle of the tube shows a transverse lumen, with many narrow fissures passing into the substance of the wall on all sides. The lumen is bounded by a continuous sheet of finely granular material,

PLATE XXI

Figure 1. The alimentary canal of *Tabanus*. ph., pharynx. oes., oesophagus. pv., proventriculus. d.c., duct of the crop. cr., crop. m.g., mid-gut. il., ileum. co., colon. mp.t., Malpighian tubes. rt., rectum. × 25.

Figure 2. Transverse section through the mid-gut of ***Tabanus***, showing the villi. t.m., circular muscle fibres. l.m., longitudinal fibres. tr., trachea. × 60.

Figure 3. Cells of the proventriculus of same, between two of the elevations in its wall, to show the external layer of eosinophil material. × 500.

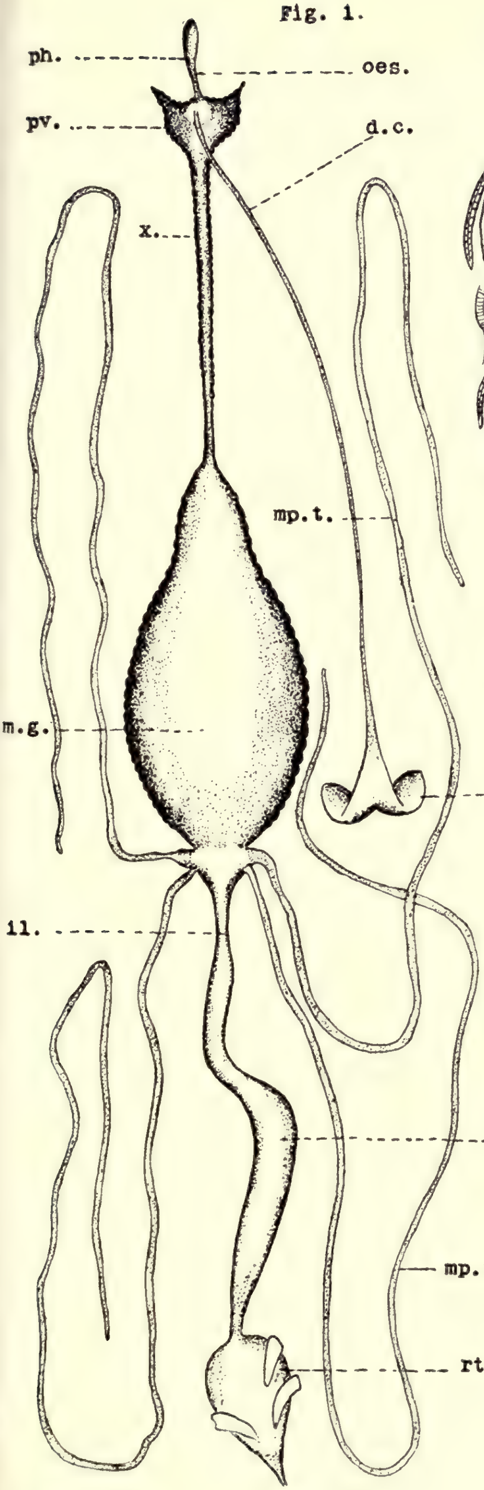
Figure 4. A section through one of the mamillæ of the proventriculus of same, showing the continuation into them of the lumen, surrounded by the eosinophile layer. The line of separation between the cells is very indistinct in this region. mu., one of the irregular muscle fibres in the wall. × 500.

Figure 5. A villus from the mid-gut of ***Tabanus***. × 250.

Figure 6. A transverse section through the proventriculus of same, about the level marked x in figure 1. × 150.

PLATE.XXI.

Fig. 1.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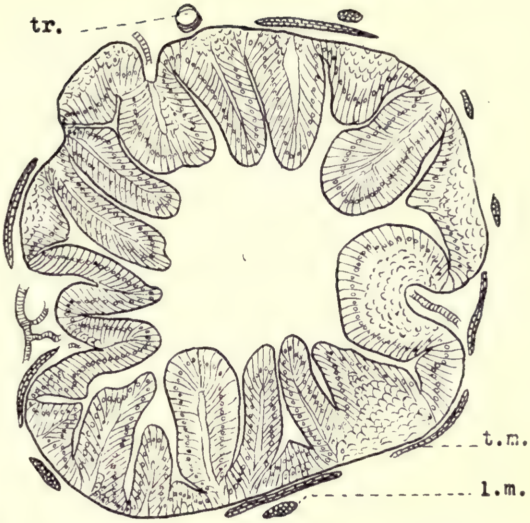


Fig. 2.

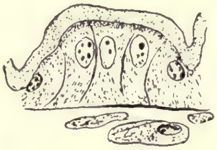


Fig. 3.

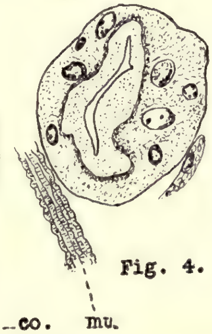


Fig. 4.

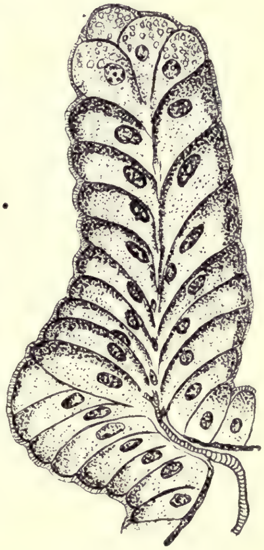


Fig. 5.

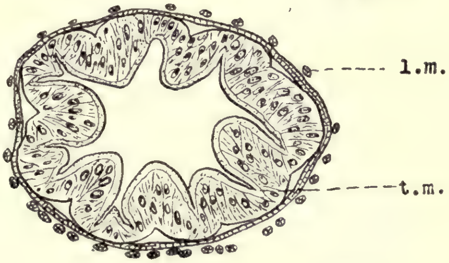


Fig. 6.

staining well with eosin and faintly or not at all with haematoxylin, which passes into all the fissures. (Plate XXI, fig. 4.) Internal to this there is a single layer of columnar cells, which are very indistinctly separated from one another, and are in many parts heaped together without any distinguishable cell membrane. The nuclei are oval or rounded, and lie near the intima. The protoplasm is finely granular, and stains uniformly, though not well, with iron haematoxylin and similar stains; there is a narrow area just underneath the intima which stains more deeply than the rest. External to these cells there is a rather thick basement membrane.

The muscular coat of the proventriculus is well developed, and consists of a large number of coarse fibres scattered all over the surface; they are arranged in an irregular manner, and not in separate circular and longitudinal bundles as is usually the case.

The mamillation of the surface is due to the heaping up of cells around the fissures, and it is especially in these elevated areas that the cell membranes are difficult to define. Each elevation consists of a mass of protoplasm with numerous scattered nuclei, with a central area of finely granular eosinophile material, in the middle of which there is a fissure which represents the lumen, and is in continuity with the lumen of the rest of the tube. The expanded portions at the anterior end are almost entirely made up of such little masses, and present a very complex picture on section. The main portion of the lumen stops short at the point where the oesophagus and the duct of the crop enter the wall, and anterior to this there are only narrow fissures communicating with one another and with the rest of the lumen.

The relations of the oesophagus, the crop, and the proventriculus are well brought out in a sagittal section. The lumen of the proventriculus appears as a narrow slit, with numerous fissures radiating from it above and below; the duct of the crop lies on the dorsal side of the proventriculus, and appears as a direct continuation of the oesophagus from the neck; it communicates with the proventriculus by an opening on the dorsal side of the latter, some distance from the anterior end.

At the posterior end the elevations become less marked, and the tube is reduced to one very similar to the oesophagus; it merges gradually with the commencement of the mid-gut.

The *mid-gut* is a large pear-shaped dilatation, with its narrowest end anterior. When it is empty the wall has a mamillated appearance like that of the proventriculus, but these markings disappear completely when the organ is distended with blood. It lies in the second and third segments of the abdomen, and is embedded in a dense coating of fat body. Next to the ovaries, it is the part of the body with the richest tracheal supply.

Mid-gut

The wall consists of a single layer of columnar epithelial cells, set on a basement membrane, and two layers of muscular fibres, an inner circular layer and an outer longitudinal one.

The layer of columnar cells is collected into numerous villi, which project into the lumen on every side, giving it a stellate appearance. In the intervals between the villi the cells are regularly columnar, but those which compose the villus are altered in shape so as to adapt themselves to its contour; the attached ends are narrowed and compressed together, while the part of the cell towards the lumen is correspondingly increased in size, its free border projecting into the lumen, and giving to the border of the villus a crenulated appearance. The basement membrane of the cells is tucked inwards at the base of the villus, and at this point a small trachea enters the wall and at once breaks up into minute branches. It is to the presence of these villi that the mid-gut owes its mamillated appearance.

The cells of the mid-gut present very different appearances at different stages of the process of digestion, and comparatively little is known about the changes which occur in them, in this or in any other blood-sucking fly, during the digestion of blood. In the resting condition, in which the fly is preparing for its meal of blood, the part of the cell anterior to the nucleus is filled up with vacuoles, of various sizes in different preparations; they may be so minute as to impart only a granular appearance to the cell, or they may be so large as to break down the cell substance. The border of the cell is striated, and in many preparations appears to be ciliated, though it is doubtful if there are really free cilia present. The nucleus is large and oval, and is situated in the posterior part of the cell in those cells which lie between the villi, but near the lumen in the rest. At the base of many of the cells a second small and deeply staining nucleus can be distinguished; this represents an immature cell which will eventually grow to replace a degenerated one.

The muscular coat of the mid-gut is of considerable thickness. The inner fibres are arranged a little obliquely, and interlace with one another. The outer longitudinal fibres are straighter, and are continuous with those of the hind-gut, the whole of the alimentary tract posterior to the proventriculus being enveloped in the same continuous sheet. At the lower end of the mid-gut, immediately above the attachment of the Malpighian tubes, there is a small dilatation, specially well provided with circular fibres, which act as a sphincter muscle.

Hind-gut

The *hind-gut* of *Tabanus* is naturally separated into two parts, an upper which is narrow and convoluted, and a lower which is wider and straight. The former, which may be termed the *ileum*, passes downwards and to the right, then transversely upwards and to the left; the wider part, or the *colon*, commences at the last turn, and from this point the gut passes directly backwards to the posterior end of the abdomen. The wall of the hind-gut (Plate XXII, fig. 5) consists of a single layer of regular cubical cells on a basement membrane, an inner layer of circular or oblique muscle fibres, and an outer layer of longitudinal ones; neither of these are very well developed. The layer of chitin which is present on the internal aspect of the cells is much thicker in the posterior part of the canal than in the ileum, and can only be distinguished with difficulty in the part near the mid-gut.

The colon is separated from the rectum by a short constriction. The *rectum* is typically pear-shaped, and opens between the last pair of dorsal and ventral plates by a narrow neck. Its wall has the same structure as that of the rest of the hind-gut, but the circular muscle fibres are much more strongly developed, and the internal chitinous layer is more conspicuous. In the wall of the rectum there are six *rectal papillae* or glands; these are stout, curved, wedge-shaped bodies, each a little shorter in its long diameter than the rectum itself. They are inserted into the wall with their broad ends directed outwards, and project a little from the outer surface through the muscular coat; their pointed ends are directed towards the anus. Each consists of a mass of large cells arranged in a radiating manner around a central lumen which opens into the body cavity, and into which there passes a small tracheal twig. The papillae occupy a considerable proportion of the total area of the lumen of this part of the gut. Their function is unknown, but they are believed to be homologous with similar structures, of common occurrence in aquatic larvae, which function as respiratory organs by absorbing air from water. In many such larvae the papillae can be protruded from the rectum at will.

In the hind-gut, from the ileum downwards, it is common to find, in this and other blood-sucking flies, a number of coarse granules of a reddish colour. These are the residue from the last meal of blood.

They are very hard and gritty, and frequently spoil sections of this part of the gut.

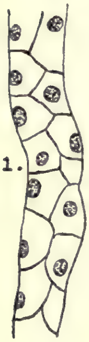
Malpighian Tubes

The *Malpighian tubes* differ somewhat in appearance in the different genera, but all conform to a general type, of which *Tabanus* may be taken as an example. There are four of these structures, opening at the junction between the mid-gut and the hind-gut. They are blind tubes of great length, at least twice as long as the body of the fly when dissected out. They lie in the abdominal cavity, and are coiled and twisted around the other organs in every direction, some appearing to pass into the posterior end of the thorax. The terminations of one pair are found near the anterior end of the mid-gut, and those of the other closely intertwined with tracheae and embedded in the fat body at the sides of the rectum. The tubes are of practically uniform diameter throughout, but are narrowed a little at the distal end. The wall is composed of large flattened cells, which are wrapped round the lumen and fitted to one another so as to form a complete tube; as a result of this arrangement only one nucleus at most is cut in cross-section. (Plate XXII, figs. 1 and 2.) The tubes are well supplied with tracheae, and are so bound down by means of them that it is difficult to dissect them out entire. In stained preparations the nuclei are very conspicuous on account of their size and of the uniformity with which they take up the ordinary stains, no discrete particles of chromatin being distinguishable. In addition to the nuclei of the cells of the tubules there are a few other smaller ones, which belong to the ultimate divisions of the tracheae distal to the terminations of the spiral thread. These are, of course, distributed all over the tissues of the insect, but are only distinguishable in situations such as this, where they are not mixed up with other cells.

The Malpighian tubules are probably excretory organs, which collect the waste products from the blood and fat body and pass them into the lumen of the intestine, from which they are passed out with the residue from the food. Their situation in many insects forms a useful landmark, but it must not be supposed that the manner in which they separate the mid-gut from the hind-gut is more than what one might perhaps term an accident. In many insects they open into the intestine much further down, as for instance in the bugs, where the opening is just above the anus.

The alimentary canal of *Tabanus* will serve as a type for the rest of the blood-sucking Orthorrapha, with the exception of the Culicinae, which show many peculiarities, and will be dealt with separately. With

PLATE. XXII.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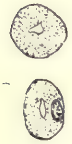
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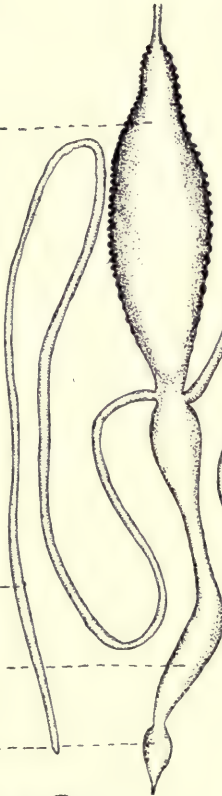
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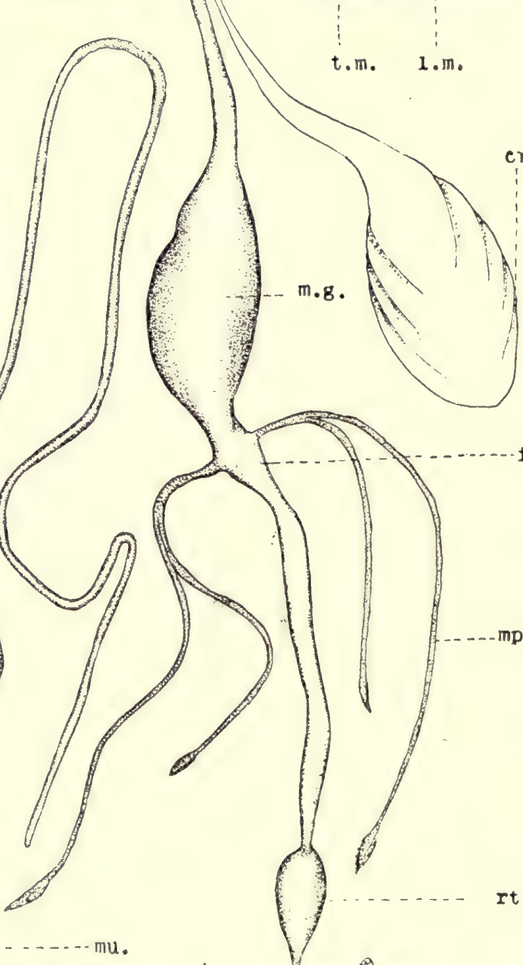
Fig. 4.
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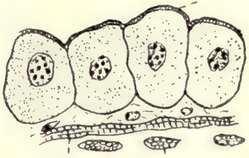


Fig. 5.

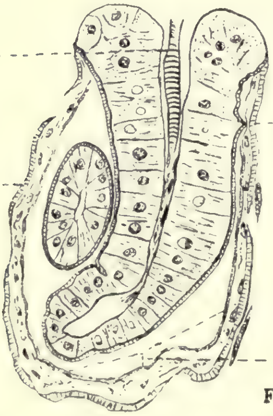
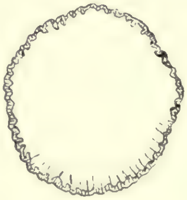


Fig. 6.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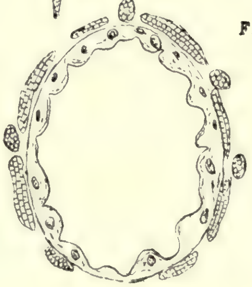
Fig. 8.

PLATE XXII

Figure 1. Apiece of Malpighian tube from *Tabanus*, showing the way the cells are wrapped round the lumen. × 100.

Figure 2. Malpighian tubes of same in section. Only one nucleus at most appears in an ordinary thin section.

Figure 3. The alimentary canal of *Culicoides kiefferi*. The crop is not shown. m.g., mid-gut. mp.t., Malpighian tubes. co., colon. rt., rectum. × 90.

Figure 4. The alimentary canal of *Phlebotomus minutus*. oes., oesophagus. d.c., duct of the crop, lying on it. cr., crop. Other letters as before. The dissection from which this was drawn was stretched a little. × 180.

Figure 5. Cells from the wall of the hind-gut of *Tabanus*. ch., the chitinous inner lamina. t.m., circular muscle, l.m., longitudinal muscle. × 800.

Figure 6. A section through the upper part of the rectum of *Tabanus*. The section was a little oblique, and shows the whole of one rectal papilla, and a part of another. tr., trachea. mu., muscle. ch., chitinous lamina in the wall. In the lower part of the section this lamina is of considerable thickness. × 70.

Figure 7. Section through the oesophagus of *Culex*, anterior end. showing the chitinous spicules which project into the interior, and the absence of cells in the wall.

Figure 8. Section through the same, lower down, in the thorax. Note the low cubical cells in the wall, and the large amount of muscle externally. The chitinous lamina is here not so well marked.

the exception of *Phlebotomus*, they have not been studied very closely, but so far as our knowledge goes they conform generally to the type seen in *Tabanus*. The proventriculus does not appear to be so well developed in any of them as it is in the latter, the oesophagus passing downwards as a simple tube to merge with the mid-gut. The digestive epithelium commences some distance anterior to the dilated part which is evidently mid-gut. The Malpighian tubules vary in their number and mode of origin. In *Culicoides* (Plate XXII, fig. 3) there is only one pair, but these are very thick, and are very conspicuous in dissections on account of their dead white colour, which is quite different to that of the hind-gut. In *Simulium* there are two pairs which arise from a very short common stem, and in *Phlebotomus* (Plate XXII, fig. 4) two pairs arising from a much longer common portion; of the two on each side one is considerably longer than the other; both terminate in slightly swollen ends.

Other Orthorraphic Flies

The crop is very well developed in *Phlebotomus*; its duct, which is an extremely fine one, leaves the oesophagus a little in front of the nape of the neck (Newstead). In *Culicoides* and *Simulium* it is not quite so large, but in none of them is it so closely connected with the oesophagus as it is in the Culicinae. It appears to function in a slightly different way to that of *Tabanus*, for both in *Phlebotomus* and in *Culicoides* it is found distended with blood in flies killed immediately after feeding, while a few hours later it is empty or nearly so. Apparently the blood is received into it from the pharynx, and passed on to the mid-gut gradually, as fast as it can be digested. The mid-gut, like that of *Tabanus*, is capable of very great distension.

The alimentary canal of the mosquito, like the rest of its anatomy, presents considerable modifications from the other Orthorrapha. The differences in the various genera, however, are not important, and for practical purposes all may be included in one description.

The Mosquito—Oesophagus

The *oesophagus* is a short and thin-walled tube which passes from the posterior end of the pharynx in the head to the anterior part of the thorax, where it joins the mid-gut. The two are separated, however, by a valvular structure believed to be the homologue of the proventriculus. The wall is composed mainly of a single layer of flattened epithelial cells, with indeterminate boundaries and small oval deeply staining nuclei. Internal to this there is a thin chitinous intima, most marked in the anterior portion of the tube, where it is provided with a set of fine spicules projecting into the lumen. The cells are more regular and conspicuous in the posterior part of the tube, where the intima is thinner. There is a thin layer of muscle fibres externally, best developed at the posterior end. The lumen of the tube may appear wide in sections, when the cells are very much flattened, or it may be contracted, in which case the cells are more cubical. Evidently the tube is capable of considerable dilatation.

The *crop* is of a totally different form to that of the other flies referred to, and consists of three sacs with excessively thin walls, termed the *oesophageal diverticula*. Two of these open into the oesophagus on the dorso-lateral aspect, and one on the ventral side. Their shape is extremely variable, as they have no rigidity of their own, and are simply adapted to the structures among which they lie. When they are dissected out of the body they contract to form irregular ovoids. Usually they are filled up with minute bubbles of gas, but in newly-hatched mosquitoes they are collapsed. The two dorsal sacs are small, and do not extend beyond the thorax as a rule, but the ventral one is very large, and passes into the abdomen, even as far as the fifth segment, and occupies a very large proportion of the abdominal cavity.

Crop or Diverticula

The wall of the sac consists of an extremely delicate chitinous intima in which a few scattered nuclei can be made out, and an external coating of extremely fine muscle fibres, which run transversely around the sac, but do not completely encircle it. The nature of the wall is best made out in sections of newly-hatched mosquitoes, in which the sacs have not been distended with air or blood.

The function of these diverticula is the same as that of the crop in *Tabanus*, with this difference, that in the mosquito the blood is retained rather longer in them. They are, in fact, true ‘ food reservoirs ’, as was pointed out by Nuttall and Shipley. In mosquitoes killed during the act of feeding they are always found to be full of blood, while a little later, depending on the rate of digestion and therefore on the temperature, the blood is almost entirely confined to the mid-gut. The great distension of the body of a mosquito as it completes its meal is not due solely to the distension of the mid-gut, but also to the distension of the diverticula of the oesophagus.

Nuttall and Shipley record some interesting observations with reference to the function of these sacs. They fed mosquitoes on a mixture of blood serum and sugar, tinted with carmine, and again in twenty-four hours on the same mixture without the colour. On dissection,

PLATE. XXIII

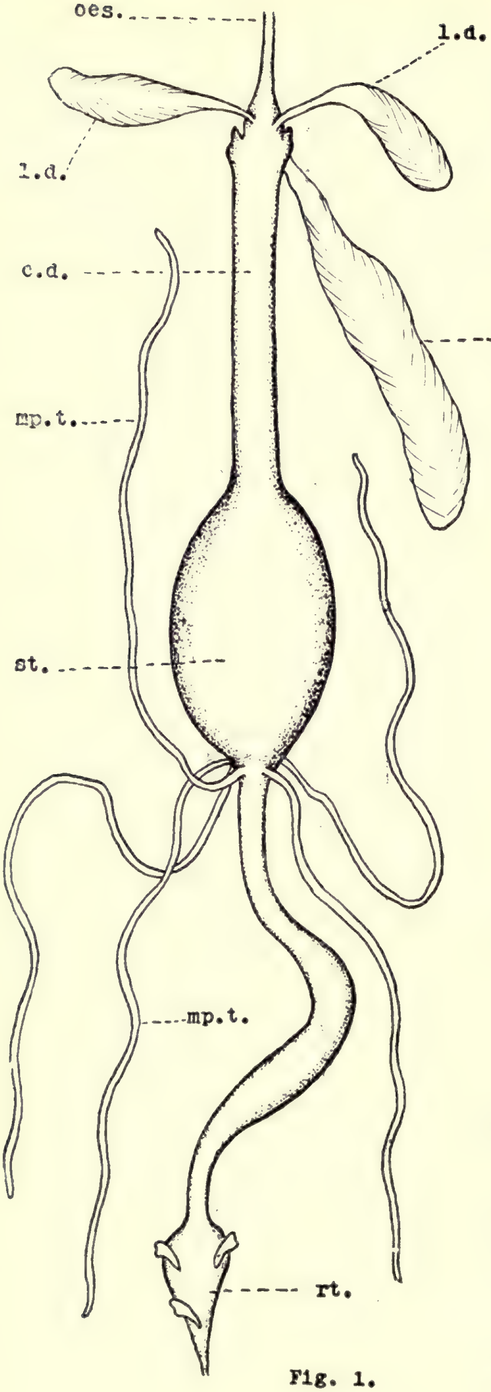
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Fig. 1.

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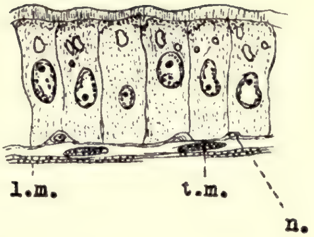

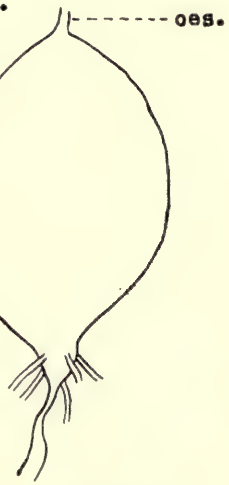

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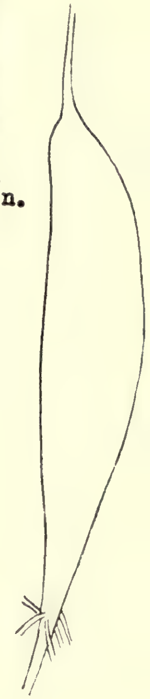

Fig. 4.

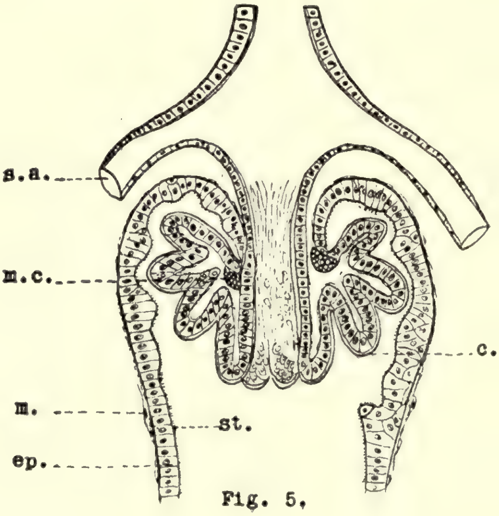
s.a.
m.c.
c.
m.
st.
ep.

Fig. 5,

PLATE XXIII

Figure 1. The alimentary tract of *Culex*, dissected out without traction. l.d., lateral diverticulum. cd., cardia. st., 'stomach': the cardia and the stomach make up the mid-gut. Other letters as before. × 80.

Figure 2. Cells from the mid-gut of *Culex*. Note the internal layer, and the vacuoles. n., nuclei lying between the bases of the columnar cells. These belong to small cells which will eventually replace the columnar ones when desquamated. × 800.

Figure 3. The mid-gut of *Culex* when distended with blood. The amount of distension may be judged by comparing the relative size of the oesophagus in this figure and in figure 1. × 30.

Figure 4. The shape of the mid-gut when dissected out by the ordinary method, involving traction.

Figure 5. Schematic longitudinal section through the commencement of the mid-gut. s.a., opening of the diverticula. m.c., sphincter muscle separating the fore-gut and the mid-gut. c., chitinous intima. st., striated border (Stäbchenschaum). m., external muscular fibres. ep., epithelium. After Schaudinn.

'the contents of the ventral sac were coloured red, that of the stomach yellow, so that there could be no doubt but that the second meal had been almost entirely taken up by the stomach'. They also confirmed this by the examination of living insects similarly fed, the coloured contents being plainly visible through the abdominal wall. Such an observation might, as they point out, have an important bearing on the development of any parasite taken up with the blood, but the fact must not be lost sight of that the conditions of the experiment were highly artificial, and it does not follow that the same result would be obtained if the experiment could be repeated with blood for both feeds. As a matter of fact mosquitoes under natural conditions will not, as a rule, feed till the last meal is completely digested, and in cold weather one frequently finds that an interval of as much as four days is necessary.

Oesophageal Valve

The *oesophageal valve*, the supposed homologue of the proventriculus, is an invagination of the posterior end of the oesophagus into the commencement of the mid-gut. It forms a marked annular thickening due partly to a great increase in the circular muscles at this point, and partly to the presence, as pointed out by Nuttall and Shipley, of small protuberances, varying apparently in number in different species, which represent the caecal appendages of the larval insect. When examined in section (Plate XXIII, fig. 5) the valve is seen to consist of a double fold of the total thickness of the wall of the oesophagus, which is tucked inside the lumen of the commencement of the mid-gut. The circular muscles which surround the canal at this point presumably act in regulating the rate of passage of the blood from the diverticula to the digestive chamber. No such valve is found in *Tabanus*, in which the blood is passed on at once into the gut, and is not stored in the crop.

Mid-gut

The *mid-gut* consists of two portions, which probably differ in their physiology as well as in their anatomy. The first part is tubular, and lies for the most part of its length in the thorax, and is continued downwards from the oesophageal valve in continuity with the oesophagus. It is a rather thick tube of uniform diameter, and is marked at its anterior end by the thickening due to the valve and the caeca. This portion is termed by Thompson the *cardia*. At the outlet from the thorax, or a little behind this, it dilates to form an oval chamber about three times the breadth of the thoracic portion. This is the 'stomach', and it is here that the blood accumulates during the process of digestion; it is here also that the parasite of malaria is most frequently found. It terminates about the fifth segment of the abdomen, and is separated from the hind-gut by a constriction at the point marked by the insertion of the Malpighian tubes.

The shape of the mid-gut of the mosquito is very markedly affected by the method in which it is dissected out of the body. In the ordinary routine method, in which it is pulled through the posterior end of the abdomen by traction applied with a needle, and by rupturing the tracheae, the sharp distinction between the cardia and the 'stomach' is lost by the rupture of some of the tissues of the wall, and although it resumes its shape to a certain extent when the traction ceases, it never assumes the shape it has when *in sitû.* The whole organ is elongated, the anterior part especially, and is correspondingly reduced in its transverse diameter; it then assumes the flask-shape so familiar in drawings of the organ. To get a correct view it is necessary to dissect away the body wall piecemeal, without pulling on the gut at all (Plate XXIII, figs. 3 and 4).

The wall of the mid-gut, both in the cardia and the dilated portion, consists of a single layer of epithelium. This is of the same type as that in *Tabanus*, but is much shorter; the cells are cubical rather than columnar, and are distributed in an even manner without villi. The borders of the cells are distinctly striated, and internal to the striations there is a more darkly staining area. Coarse granules and vacuoles are usually present, and the rest of the protoplasm shows fine granulations. There is little difference to be observed between the cells in the narrow part and those in the dilated portion, except that those of the latter are higher. As in *Tabanus*, the cells become flattened when the gut is filled with blood.

External to the cells and their basement membrane there is a layer of circular muscle fibres, and external to this some scattered longitudinal ones. The circular fibres are well marked at the lower end of the gut, where they form a sphincter which separates the mid-gut from the hind-gut.

The *hind-gut* resembles that of *Tabanus* so closely that there is no need for a detailed description. The Malpighian tubes possess but one peculiarity, that in *Culex* there are five of them instead of four.

Alimentary Canal in the Cyclorrapha.

The alimentary canal in the Cyclorrapha is much more complex and highly organized than in the Orthorrapha. In the first place, its length is very greatly increased, while at the same time there is no dilated portion representing the mid-gut as seen in *Tabanus* and in the mosquitoes. The effect of this increase in length and diminution in diameter must obviously be an advantageous one, for it exposes a larger surface of digestive cells, and at the same time reduces the distance by which the central particles of food are separated from the gut wall. The increase in length, which is confined to the mid-gut, has necessarily resulted in throwing the tube into many convolutions. The proventriculus has assumed a definite shape common to all, and forms a valve separating the fore-gut from the mid-gut.

The most striking development is the formation of a second tube internal to the epithelium, by which the food contained in the gut is separated from the digestive cells. This structure is known as the *peritrophic membrane.* It is found in many other insects, and also in their larvae, and indeed it is somewhat remarkable that it should be absent in the Orthorraphic flies.

The form of the alimentary canal in the Cyclorraphic Diptera is remarkably constant in the different genera, such differences as there are being mainly in the length of the tube and the complexity of the coils. That of *Philaematomyia* will serve as a type; the parts in some other members of the group will be referred to subsequently.

Philaematomyia—Oesophagus

The *oesophagus* is a short tube which passes through the neck from the posterior end of the pharynx to the anterior part of the thorax. At its commencement it is of considerable width, but it very soon contracts to form a narrow tube which passes through the brain and neck. The structure of the wall is the same as that of *Tabanus,* except that there is rather more muscular tissue.

As it passes into the thorax the oesophagus lies ventral to the proventriculus, and comes into close contact with it. The two communicate by an opening which is directed upwards and slightly backwards; immediately posterior to this point the duct of the crop commences, and runs backwards into the abdomen ventral to the gut. The oesophagus and the duct of the crop appear in fact to form a continuous tube, closely pressed against the proventriculus; the communication between it and the proventriculus is only revealed by sections.

Crop

The *crop* is a large and thin-walled sac like that of *Tabanus,* situated in the anterior portion of the abdomen. When empty it is contracted, but when the fly has just finished feeding it is distended with blood, and may occupy a considerable proportion of the abdominal cavity. Its wall is thicker than that of the corresponding organ in the Orthorraphic flies, both the muscular and cellular portions being more conspicuous.

It will be noted that the positions of the crop and the proventriculus are the reverse of those in *Tabanus*, a fact which throws some light on the development of the parts. It seems probable that in some remote ancestor the crop was a simple dilatation of the oesophagus, such as is found in many modern insects, and that this dilatation became divided into several portions, one or more of which passed backwards towards the abdomen, remaining connected with the oesophagus only by a narrow duct. In *Tabanus* the crop has developed from a dorsal sacculation, in the Muscidae from a ventral one. In the mosquito the development is seen at an early stage, in which three of the original sacculations are present, one of them, the ventral, being predominant, and extending to the abdomen when distended. All these structures function in the same way, receiving the blood from the pharynx and passing it on to the mid-gut for digestion, but the rate at which the crop is emptied seems to differ in the different forms. In some, as in *Tabanus*, the contractions of the crop appear to be as rapid as those of the pharynx, so that the blood is passed on to the gut at once, while in others, among which are *Musca* and *Philaematomyia*, the food is retained for a time, and passed on gradually. The object of the crop is to enable the fly to absorb a very large amount of food at one time—evidently a great advantage in the case of those flies which do not remain permanently in association with the host on whose blood they feed.

Proventriculus

The *proventriculus* is a small disc-shaped body, flattened from above downwards, but placed rather obliquely in the thorax, with its lower edge directed downwards and forwards. The dorsal surface is smooth and convex; the ventral surface is irregular on account of the attachment of the oesophagus and the duct of the crop.

The structure of the proventriculus is best understood from the study of a longitudinal section, such as that shown in Plate XXIV, fig. 2. It consists of a mass of cells, part of which are derived from the mid-gut and part from the fore-gut. The external layer is continuous with the mid-gut and is composed of columnar cells which are longest in the anterior portion. Inside this there is a thick plug of smaller round cells which belong to the fore-gut. The oesophagus is, in fact, tucked inside the dilated end of the mid-gut, the portion which is invaginated having a greatly thickened wall. The opening by which the oesophagus and the mid-gut communicate lies in the middle of this plug, and is not shown in the section figured, as this is not precisely through the middle line. The invaginated portion is button-shaped, and, since the mid-gut is attached to it at some distance from its periphery and on the anterior side, there is an annular recess between the edges of the plug and the anterior end of the cells belonging to the mid-gut. It is in this recess that the peritrophic membrane arises.

The structural arrangements at the communication of the oesophagus with the mid-gut are evidently adapted to function as a valve to prevent regurgitation of the contents of the gut. Pressure of fluid in the anterior end of the mid-gut would result in dilatation of the annular recess, and would, therefore, compress the sides of the opening of the oesophagus. A sphincter muscle has been described in this region in *Musca*. Its presence would not appear to be necessary for the efficient working of the valve.

Mid-gut

The *mid-gut* is an elongated tube, extending from the proventriculus in the thorax to the distal portion of the abdomen. It is many times the length of the cavity in which it lies, and is thrown into many coils and twisted upon itself in order to accommodate its shape to the space available. It is to the length of the mid-gut that the elongation of the alimentary tract is due, for the fore-gut and hind-gut are relatively no longer than those in the Orthorraphic flies. The coils in *Philaematomyia* are closely similar to those in *Stomoxys*. The separate turns are held loosely in position by the tracheae which supply them with air.

The mid-gut may be conveniently divided into three portions. The first of these is a narrow tube immediately posterior to the proventriculus, which passes directly through the thorax without convolutions. This expands after a short course to form the portion known as the *ventriculus*, or *chylific ventricle*, which is the widest part of the gut; it lies in the posterior part of the thorax and in the abdomen, and is twisted into a double coil in its posterior part. The third part, corresponding to rather less than half the total length of the mid-gut, is known as the *proximal intestine*, a rather unfortunate term; it should not be confused with the hind-gut. It is about half the diameter of the ventriculus, and is more loosely coiled. At its posterior end the Malpighian tubes enter the gut.

The wall of the mid-gut is lined throughout with a digestive epithelium similar in its general appearance to that of *Tabanus*. The cells are arranged in a single layer, and vary in height, the largest cells being found in the ventriculus. Those lining the narrow anterior portion of the gut are regularly cubical (Plate XXV, fig. 3). In the ventriculus, and to a lesser extent in the proximal intestine, the wall is in many places raised into small protuberances, between which there are shallow fossae. In many sections one finds the cells undergoing changes connected with the process of digestion, and discharging their contents into the lumen. (Plate XXV, fig. 4.)

External to the cells there are circular and longitudinal muscle fibres, both of which are well developed.

Hind-gut

The *hind-gut* is similar to that of *Tabanus*, and is of about the same length in proportion to the size of the fly. It is of uniform diameter, but has a slight constriction about its middle point, where the circular muscle fibres are strongly developed so as to form a sphincter. At the distal end it opens into a rectum like that of the Orthorraphic flies, with four rectal papillae.

The structure of the wall of the hind-gut is simple. There is a single layer of regular cubical cells, with a chitinous intima which is best developed in the posterior portion, and external to this the usual two layers of muscle, of which the circular fibres are the most strongly developed. The chitinous intima in the lower part is developed into a series of short spines, which project into the lumen of the gut, and are directed towards the anus. (Plate XXIV, fig. 3.)

Malpighian tubes

The *Malpighian tubes* arise on each side by a common stem, and pass forward and backward among the tissues. Like those of *Tabanus* they are composed of a single layer of cells, but the individual cells are rounder, and their central portions project a little from the surface, thus giving to the tube a wavy contour. At the distal end, for about one-quarter the length of the tube, the lumen is dilated and filled with a densely white granular material, which stretches the cells composing the wall and distorts the regular arrangement found in the lower portions. The dilatation is most irregular, so much so that this part of the tubule appears to consist of a series of elongated pouches connected together by narrow necks. The wall is here very fragile and easily ruptured. The degree to which the tube is distended and filled with this white material varies in different specimens, and probably depends on the age of the fly.

Peritrophic membrane

The *peritrophic membrane* (Plate XXIV, figs. 4 and 5), already referred to, forms an inner tube which extends from the proventriculus to the anus, and completely separates the contents of the gut from the epithelium. It hangs down from the proventriculus, in fact, like a tubular curtain, and is in contact with the cells at all points but nowhere attached to them except at its upper end. It is composed of an extremely thin and translucent material which is very

PLATE XXIV

Figure 1. The alimentary tract of *Philaematomyia insignis*. c.v., chylific ventricle, or first part of the mid-gut. p.i., proximal intestine. pv., proventriculus. sp., a thickening of the circular muscle of the gut wall, probably acting as a sphincter. h.g., hind-gut. Other letters as before. × 12.

Figure 2. A longitudinal section through the proventriculus of *Philaematomyia insignis*, showing the origin of the peritrophic membrane. j., the junction of the fore-gut and the mid-gut. oes., the invagination of the oesophagus into the mid-gut. f.g., fore-gut. c., commencement of the mid-gut. pt.m., peritrophic membrane.

Figure 3. Cells from the hind-gut of *Philaematomyia insignis*, showing the chitinous spines.

Figure 4. A diagrammatic section through the mid-gut of a Muscid fly to show the peritrophic membrane *in sitû*. m.c., the cavity of the mesenteron. ep., epithelium of digestive cells. pt.m., peritrophic membrane.

Figure 5. A diagrammatic longitudinal section of the alimentary tract of a Muscid fly, to show the relations of the peritrophic membrane. Lettering as before. This and the last figure after Berlese, slightly modified.

Figure 6. A portion of the distal end of the Malpighian tube of *Philaematomyia insignis*. × 150.

Figure 7. A portion of the proximal end of the same. × 150.

Figure 8. The alimentary tract of *Glossina*, *in sitû*. ph., pharynx. oes., oesophagus. c.cg., the common salivary duct, formed by the union of the two ducts. c.j., duct of the crop. j., the crop. pr., proventriculus. i.th., thoracic portion of the intestine. i.m., abdominal portion. a.r., rectal ampulla. gl.s., salivary glands. r., rectum, or hind-gut. p.r., rectal papillae. From Rouband, after Minchin.

PLATE. XXIV.

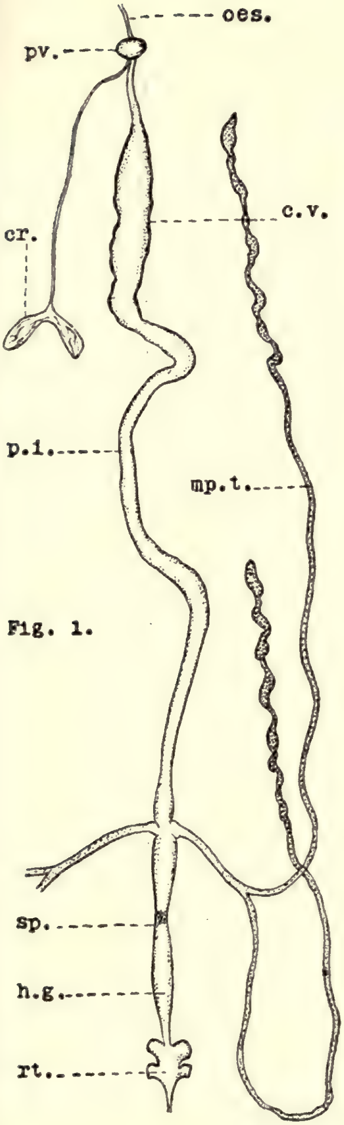
oes.
pv.
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Fig. 1.

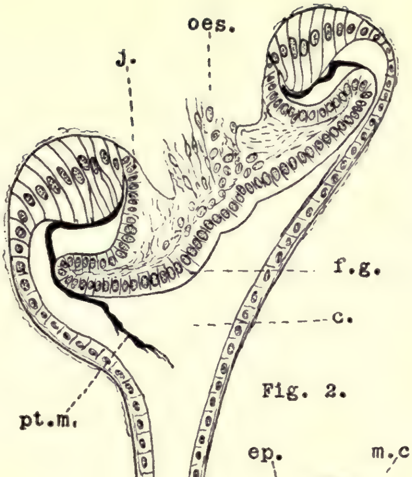
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Fig. 2.

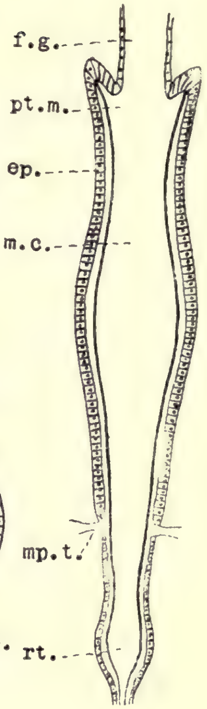
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Fig. 5.

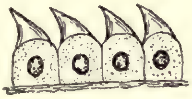

Fig. 3.

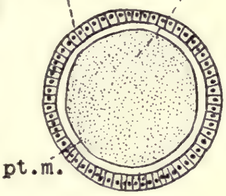

Fig. 4.

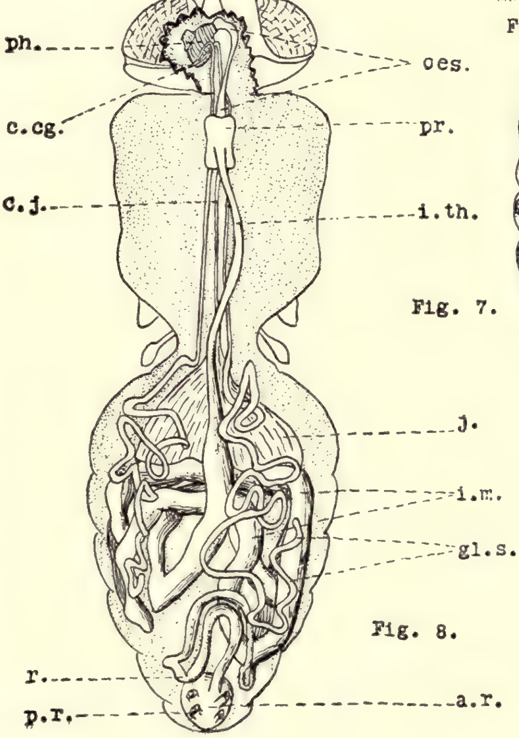
ph.
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Fig. 8.

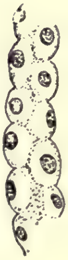
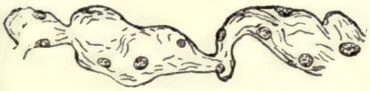


Fig. 7.

Fig. 6.



delicate and easily ruptured, but which possesses sufficient coherence to enable one, by careful dissection, to draw out a considerable portion of it intact and containing the food.

The significance of this membrane will be evident from its relations. It is a continuous sheet with no apertures, and therefore the digestive fluids from the cells, and the digested products from the food, must pass through it as through an osmotic membrane.

The peritrophic membrane, according to Berlese, is composed of chitin, secreted by special cells situated at the junction of the proventriculus with the mid-gut, to which is added a deposit of mucous substance secreted by the cells of the mesenteron. It appears to grow downwards from the mesenteron till it reaches the anus.

Musca

The alimentary canal of *Musca* is very similar to that of *Philaematomyia*. The mid-gut is a little longer and more convoluted, and the ventriculus broader. The latter is narrower at its anterior end than elsewhere, but it is not separated from the proventriculus by a definite neck as is the case in *Philaematomyia*, so that almost the whole of the part lies in the thorax. The Malpighian tubes are not usually dilated at the ends and are often of a yellowish or greenish colour. It is rather remarkable that the colour of the tubes should differ in different species.

It should be noted that the part of the gut sometimes referred to as the 'distal intestine' is the hind-gut. The proximal intestine belongs to the mid-gut or mesenteron.

Stomoxys

The alimentary canal of *Stomoxys* is like that of *Philaematomyia*, and is of about the same length. The narrow portion anterior to the dilated ventriculus is longer, and extends through the thorax. This is, in fact, a peculiarity found in all the blood-sucking Muscids which have been examined, and is probably related to their habit of taking in a large meal at one time. The Malpighian tubes show an interesting feature, first pointed out by Tulloch in the case of *Stomoxys*, but probably of common occurrence, namely, that the dilated distal ends of one pair pass to the dorsal region and lie in a constant position near the heart and pericardial cells. As these two tubules arise by a common stem, it is possible, as suggested by Minchin, that the tubes should be regarded as dorsal and ventral, not as lateral.

In *Glossina* there is a great elongation of the mid-gut, which has brought about a corresponding complexity in the coils into which it is thrown. The proventriculus, according to Minchin, is saddle-shaped, that is to say, concave longitudinally and convex transversely when seen from above. Its lateral portions are wrapped round the oesophagus and the duct of the crop, which therefore appear to be embedded in the substance of the organ. The crop is relatively large, and is always found to be full of fresh blood when the fly has had a full meal. When the fly has not fed recently the crop contains bubbles of gas.

Glossina

In all these flies it is the anterior portion of the mid-gut, or the ventriculus, in which the fresh blood is found after feeding. The narrower portion posterior to this, which, following the usual nomenclature, has been termed the proximal intestine, frequently contains a darker and more viscid material composed of partially digested blood.

Hippobosca

In *Hippobosca* and *Melophagus* the alimentary tract presents a striking peculiarity in the absence of a crop, a condition of affairs which is correlated to their method of feeding. *Hippobosca* does not fill itself with blood at one puncture, but flits about from place to place on the skin of the host, remaining with it for long periods. Indeed, it is rare to find a fly of this genus apart from its host, which it does not leave even for copulation. *Melophagus*, which is wingless, cannot leave the host at all during the active period of its life, but is associated with it after the manner of the fleas. In neither case is there any necessity for the fly to take a large meal, and consequently there is no necessity for a crop.

The proventriculus in *Hippobosca* is represented by a small oval swelling on the anterior portion of the gut. The mid-gut is very long and is twisted into many coils, and has the same general character as that of *Musca*. The anterior portion is much thicker than the rest, though the gut as a whole is wider than that of any of the other flies referred to. The rectum is large and capacious, and generally contains a milky fluid. Its wall is thick and leathery, and of a dark brown colour, quite unlike that of *Musca*.

There are four Malpighian tubes, which arise independently from the gut. They are simple and of a uniform diameter, and have not the bead-like appearance of those in the Muscidae, and are distinctly narrower. The hind-gut posterior to their origin is slightly swollen; it contracts again at the point where it joins the rectum.

In the foregoing the term 'hind-gut' has been used in the sense in which it is ordinarily understood, as that part of the alimentary tract posterior to the openings of the Malpighian tubes. The actual extent of the posterior invagination, which is lined by a chitinous intima, is not as

PLATE XXV

Figure 1. The hind-gut of *Hippobosca maculata*, showing the openings of the four separate Malpighian tubes and the rectal ampulla. v., sphincter muscle at the opening into the ampulla. d.i., distal intestine. mp.t., Malpighian tubes. × 36.

Figure 2. A transverse section through the posterior part of the abdomen of *Haematopota pluvialis*. The section from which this was drawn was not cut in an absolutely transverse plane, so that the two sides are not symmetrical. t.m., circular muscle fibres, connecting the tergite and sternite. f.b., fat body. l.m., longitudinal muscle fibres, connecting the adjacent tergites and sternites respectively. h., heart and pericardial cells. h.g., hind-gut, cut in three places on account of its twist. ov., ovaries: the several tubules are cut at different levels, some through the nurse cells, the nuclei of which are conspicuous. a.g., accessory glands of the reproductive organs. × 66.

Figure 3. Cells from the upper part of the mid-gut of *Philaematomyia insignis*, a short distance below the proventriculus. × 500.

Figure 4. Cells from the middle portion of the mid-gut of the same. × 450.

Figure 5. Longitudinal section through the abdomen of *Philaematomyia insignis*, to one side of the middle line. ha., haematocoele, always apparently a large space in sections, on account of the unavoidable shrinkage. d.i., portions of the distal intestine cut through obliquely. ch.t., abdominal tergite. r.p., rectal papilla. rt., rectum. c., a mass of cells around the rectum, most of which belong to the proximal ends of the Malpighian tubes. mb., the membraneous portion of the ventral wall, which is only chitinized in the middle line. p.i., proximal intestine. sl.g., salivary glands. ch.v., chylific ventricle. m.ph., mesophragma. pv., proventriculus. Note the large number of circular muscle bundles. × 69.

Figure 6. The rectum of *Musca*, showing the tracheæ entering the rectal papillæ. × 66.

PLATE. XXV.

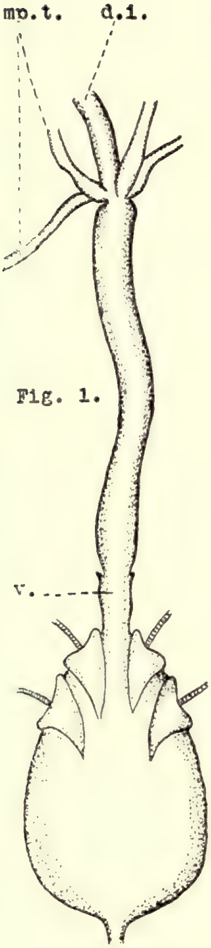
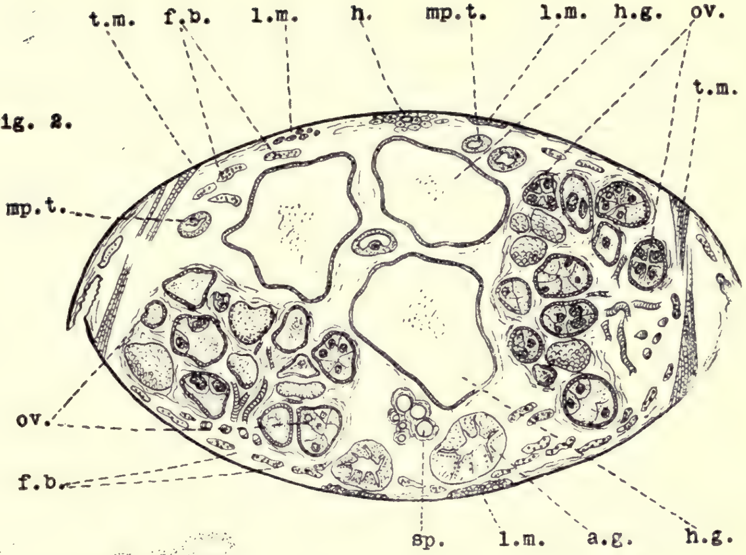


Fig. 1.



t.m.
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l.m.
h.
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Fig. 2.

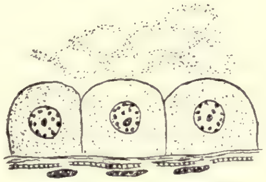


Fig. 3.

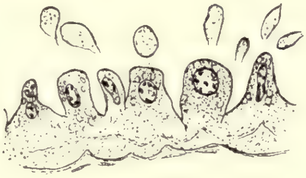


Fig. 4.

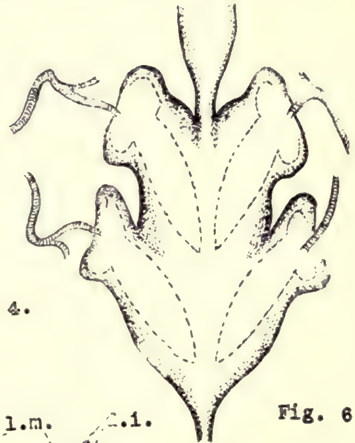
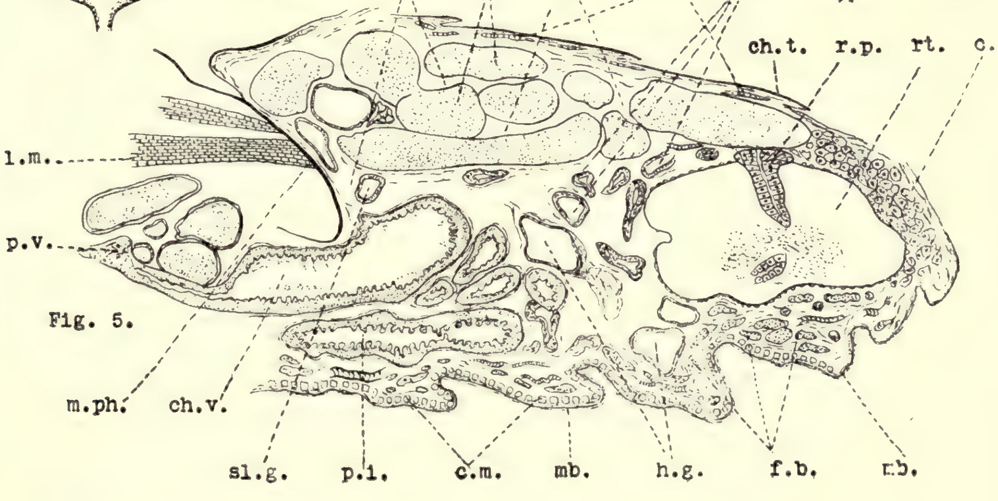


Fig. 6



ha.
mp.t.
ha.
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rt.
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l.m.
p.v.
m.ph.
ch.v.
sl.g.
p.i.
c.m.
mb.
h.g.
f.b.
mb.

Fig. 5.

yet definitely ascertained for the various Muscidae. It could only be found by a very carefully prepared series of sections of the whole of the hind part of the tract. The appearance seen in a recently fed fly suggests that the extent of the digestive portion is actually less than the terms used indicate.

The Salivary Apparatus

The *salivary apparatus* consists of *glands* situated in the thorax, extending in some cases to the abdomen, *ducts* to convey the fluid from them through the neck, a *reservoir* or *valve* situated in the head, and an *efferent duct* along which the saliva flows into the wound. The distal part of the apparatus has already been described in connection with the mouth parts. The thoracic salivary glands in the Diptera correspond to the lingual glands in other insects. The labial glands are present only in *Musca* and its near allies, and in *Tabanus*; they have been described as they occur in *Musca*, and need not be further referred to here, except to remark that their existence should not be forgotten when considering the possible modes of exit of a parasite from the body of a fly.

Function of saliva

Regarding the nature and use of the saliva we have little information. It has been frequently stated, with little evidence, that its purpose is to prevent the coagulation of the blood during its transit from the host to the alimentary tract of the fly. It has also been suggested that the effect of the secretion, by producing the familiar inflammatory phenomena, is of value to the insect in that it facilitates the flow of blood. It has been shown by Nuttall and Shipley that the salivary glands of *Culex*, when emulsified, possess neither the power of haemolizing the blood in the mid-gut, or of preventing clotting. In the case of *Tabanus* the blood corpuscles are intact and apparently uninjured up to at least seven minutes after feeding.

All the Diptera which habitually suck the blood of man undoubtedly have in their saliva some substance which produces a painful inflammation, and it is remarkable how different individuals react to this substance. With the mosquito, people living under identical circumstances will exhibit widely different degrees of reaction, judged both by the visible effects and by the amount of irritation induced. Some degree of immunity appears to be established after a time, and the person, though bitten as frequently as before, suffers much less from the individual bites, many of which he barely notices. The fact that an old inhabitant suffers less from insect bites than a new arrival in the tropics is much more likely to be accounted for by the lesser degree of reaction than by any actual dimunition in the number of bites inflicted.

A similar idiosyncrasy is to be noticed with regard to other insects. Many people suffer acutely from the bites of Tabanids, which in the majority of cases produce only a momentary irritation and some rubifaction. The same thing has been noticed with *Simulium.*

The Glands

The *salivary glands* of the Diptera are usually tubular and elongate, though great variation in their length is met with in the order. The blind end is often a little dilated, giving it a saccular appearance, and possibly enabling it to retain a quantity of saliva. The glands may extend through the thorax, and be twisted into many convolutions on account of their length, or they may be confined to the anterior part of the thorax. The increase in the length of the glands corresponds with other anatomical points which indicate a high degree of specialization. For instance, in *Phlebotomus* they are short and round, while in *Glossina* they are extremely long. The increase in length gives, of course, a greater extent of secreting surface, as was pointed out in connection with the alimentary canal.

Culex and Anopheles

The salivary glands of mosquitoes are of particular importance since it is in them, in certain species of *Anopheles,* that the parasite of malaria is to be found previous to its entrance into the blood of man. They are of the tubular type, and are confined to the thorax of the insect. Certain differences between the glands in *Anopheles* and *Culex* (Plate XXVII, figs. 7 and 8) have been emphasized by Christophers and by Nuttall and Shipley.

There are three glands on each side, lying in the lower part of the anterior end of the thorax, immediately above the first pair of legs. They are just below the main mass of thoracic muscle, and lie embedded in fat body. The ducts meet in a common point as they emerge from the substance of each gland, and lead by a common duct to the neck, where those of the two sides unite in the region of the occiput, and under the sub-oesophageal ganglion, to form a single channel, which passes to the salivary pump described in connection with the mouth parts.

Each acinus is an elongate tubule, within which, in the fresh state, the intra-acinar duct can be seen. Of the three acini on each side the one which lies between the others, and appears dorsal to them in cross sections of the anterior part of the thorax, is slightly smaller than its fellows. All the glands consist of a single row of cubical or short columnar cells arranged around a central lumen, which is constituted by the intra-acinar duct. Outside the cells there is a well-defined basement membrane. At times small secondary acini or bifurcations of one or other of the three glands are met with.

The lateral glands, which are of what Christophers terms the 'granular' type, are generally almost filled with a granular secretion, which compresses the protoplasm and the nucleus of the cell towards the outer border. In the fresh condition the secretion is clear and refractile, while in sections it appears as a coarse reticulum, due, as pointed out by Christophers, to a precipitation of the secretion by the fixative. It does not stain with eosin, and only faintly with haematoxylin. There is some reason to believe that the portion of the gland adjacent to the junction of the three ducts is different to the rest, for Grassi notes that its secretion is more refractile, while Christophers states that the cells in this situation are smaller, and the lumen of the gland correspondingly restricted. In some species of *Culex* the reverse is the case, the cells in this region being cylindrical; there is, however, a good deal of difference in different species and individuals in the appearance of the glands.

The central glands are of what Christophers terms of the 'colloid' type. The cells are not so much compressed, and contain more protoplasm than those of the lateral glands. Unlike that of the latter, the secretion stains well with eosin and also with haematoxylin; it is less refractile in the fresh condition.

The appearance of the intra-acinar duct differs a little in *Culex* and *Anopheles*. In the former it is of the same width throughout, and terminates near the blind end of the gland, while in *Anopheles* it terminates in an indefinite manner about the middle, so that the upper portion of the gland is expanded and forms a reservoir for the storage of saliva. The main ducts give off a few small lateral branches, which end blindly. Under a high magnification minute pores can be seen in the chitinous wall of the ducts.

Little or no change takes place in the glands as a result of feeding; it is probable that only a small amount of saliva is passed down at each bite, and that it is very rapidly replaced by the secreting cells.

In newly hatched and unfed mosquitoes the cells of the gland are much more regular, and the nucleus is little if at all compressed by the secretion. In this condition the nucleus stains very deeply and is placed centrally. The protoplasm distal to the nucleus contains many very fine granules and one or two vacuoles.

The salivary glands of *Phlebotomus*, as described by Newstead, lie in a position corresponding to those of the mosquito. There is only one pair of glands at each side. They are pear-shaped structures, composed of a single layer of remarkably large cells surrounding a central lumen.

Tabanus

In the Tabanidae (Plate XXVII, fig. 9), the glands are long and tubular, and extend into the anterior part of the abdomen. They lie in the lower part of the thorax slightly below and on either side of the proventriculus for the most of their length, and turn outwards a little at their distal ends, which are somewhat dilated. The lumen of the glands contains a fine granular eosinophile material when seen in stained sections. The wall is composed of a single layer of cubical or short columnar cells, with well defined nuclei, which are never compressed like those in the salivary glands of mosquitoes. The chromatin of the nuclei is divided up into a number of sharply separated particles. The cells have a well defined basement membrane, which is well demonstrated when fresh specimens are ruptured.

Muscidae

In the Muscidae the glands are always long, and extend into the abdomen; they may, as in *Glossina* (Plate XXIV, fig. 8), be much coiled. They are recognized at once on opening the abdomen by their glistening white colour, which is quite unlike that of the gut or the Malpighian tubes. They are attached to the surrounding organs by many tracheal twigs, and cannot be drawn out through the neck without rupturing unless they are first freed from their attachments.

The only differences in the different genera are in the length. *Glossina* appears to have the longest, though those of *Philaematomyia* are also very long. *Stomoxys* has rather short glands, shorter than those of *Musca*. The glands are so similar in structure to those of *Tabanus* as to call for no further description.

The relationship of the salivary glands to the surrounding structures should be noted. They lie, as do the other organs, free in the haematocoele, and are bathed by the blood. Those flies which have long glands extending into the abdomen have also long and coiled alimentary tracts, so that the wall of the gut and the wall of the glands are in contact at many points, as can be readily shown by sections. Should any parasite, motile or otherwise, pierce the wall of the gut and thus become free in the haematocoele, there is therefore every chance that it may also pierce the wall of the gland. No special selective faculty on the part of the parasite need be assumed.

DIGESTION AND ABSORPTION

Our knowledge regarding the nature and mechanism of the processes by which food material ingested by the insect is converted into assimilable substances and used up in nutrition is unfortunately very scanty. Packard, writing fifteen years ago, devoted only six pages to the subject, while Berlese's recent voluminous work contains little more. Neither entomologists or parasitologists have given special attention to the case of the digestion of blood, and even Schaudinn, who recognized the importance of the matter, touched on it only incidentally, without giving any account of the histological appearances. It must be remembered, however, that the changing conditions met with in the alimentary tract during digestion constitute the environment of ingested parasites, and have therefore a special importance from the present point of view. The following account is by no means as full as the importance of the subject demands.

Function of mesenteron

The part of the alimentary tract which is specially concerned with digestion and absorption is the mid-gut, or mesenteron, which is equipped for this purpose with a secreting epithelium, the cells of which are usually columnar and have no chitinous intima. The secretion is passed out into the lumen of the gut, where it mixes with the food, resolving it into soluble substances, which are then taken up by the cells and passed into the body cavity. Phagocytosis of food particles does not take place. The fore-gut, derived from the stomodaeum, serves as a channel to pass the food from the mouth to the digestive chamber, and is modified in various ways, as has already been pointed out, to regulate the flow, and in certain cases to act as a food reservoir. In many mandibulate insects, such as the cockroach, the part of the fore-gut immediately anterior to the mid-gut is dilated to form a chamber termed the crop, into which open certain gland-like organs, the caeca. In this chamber a preliminary digestion takes place, the inlet into the mid-gut being meanwhile shut off by a strong sphincter muscle. In blood-sucking insects, however, digestion is confined entirely to the mid-gut, and the crop serves at most as a temporary reservoir for the food. Instead of appearing only as a simple dilatation of the oesophagus, it may be separated from it by a long duct, the receptacle itself being situated in the abdomen. As will be shown presently, the cells of the posterior part of the stomodaeum have also the function of providing a covering layer for the fluid food on its entry into the mid-gut.

Digestion in the crop

The posterior portion of the tract, derived from the proctodaeum, serves only to conduct the residue resulting from the digestive process, and the secretion of the Malpighian or urinary tubules, to the exterior.

Salivary glands

The salivary glands probably provide some secretion which is concerned in digestion, directly or indirectly. Little is known regarding its exact properties or function, but one thing is evident from anatomical considerations, namely, that in blood-sucking insects it is necessary for the saliva to be conveyed to the wound. The salivary system does not come into communication with the alimentary tract anywhere except at the prestomum. In the Diptera the conveyance of the saliva is arranged for by the elongation of the hypopharynx ; in the Hemiptera and Siphonaptera, as will be explained in later chapters, the same end is attained by different means.

Significance of the peritrophic membrane

It has been stated that solid particles are not ingested by the cells of the mid-gut, that is, that the food substances are rendered soluble before they are absorbed. The proof of this lies in the presence of the peritrophic membrane, which has already been described as it occurs in the alimentary tract of *Philaematomyia*. The presence of such a structure, completely separating the cells of the gut from the ingested particles, renders necessary the assumption that the soluble products of digestion arrive at the cells after passing through the membrane.

In the Muscid flies, as in many other insects and their larvae, the peritrophic membrane is a well-defined structure, which possesses sufficient cohesion to enable one to separate it from the gut wall, and passes to the distal end of the tract. In the Orthorraphic flies, on the other hand (at least in *Culex* and *Tabanus*, which have been carefully examined), no such definite membrane exists, there being only a delicate layer of homogenous tissue, which stains faintly with eosin, between the blood in the gut and the cells ; this layer is so fine that it can only be distinguished under the most favourable conditions. According to Schaudinn, who noted its presence in the mosquito, it is formed as a secretion of the chitinogenous cells of the fore-gut, given off by them as the fly feeds, and passed into the mid-gut as a protecting envelope surrounding the mass of blood. But in these Orthorraphic flies the gut is a distensible organ, and is increased to many times its normal diameter when the insect has ingested a full meal, and the layer of secretion, only a thin one at the most, becomes so thinned out by the stretching of the wall that it can no longer be recognized. It can, as was pointed out by Schaudinn, be

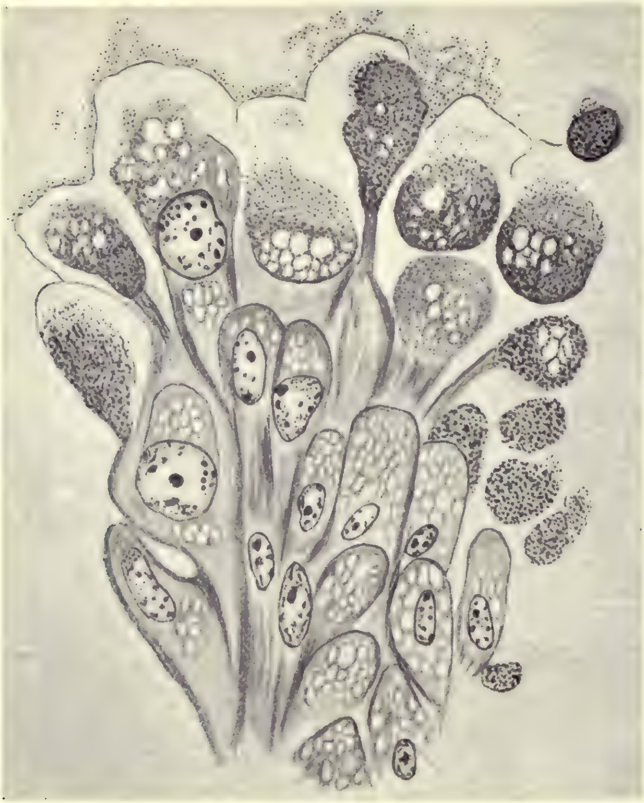

Fig. 1.

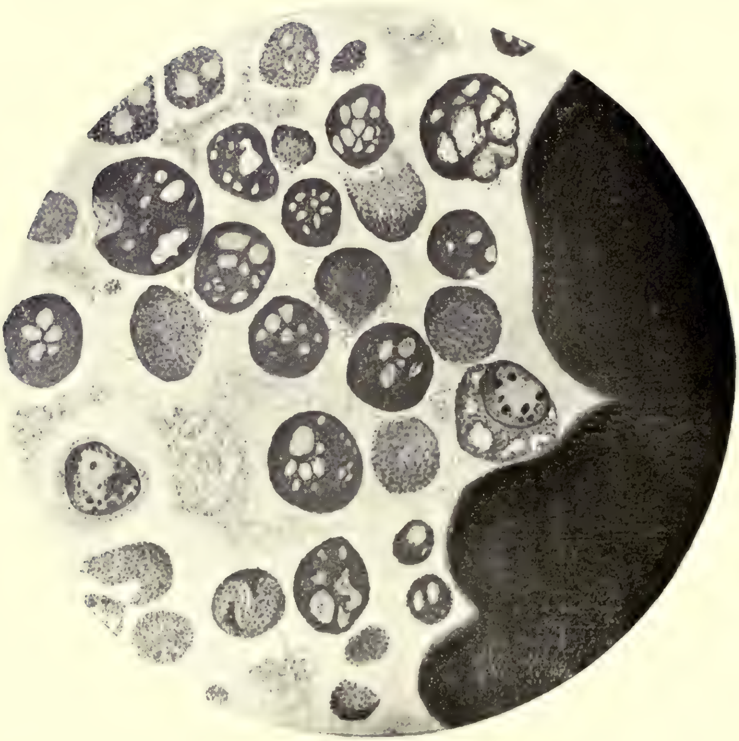

Fig. 2.

PLATE XXVI

Figure 1. A villus of the mid-gut of *Tabanus*, immediately after the first meal of blood. The deeper cells are highly vacuolated, while the ones nearer the lumen are discharging their contents into it, and are disintegrating.

Figure 2. A section through the same gut, at a lower level, and nearer the centre. The dark area on the right of the drawing is blood pigment, derived from the digestion of the layer of blood which has been in contact with the epithelium. The rest of the lumen is filled up with disintegrating cells, loaded with granules. In some the nucleus, in varying stages of disintegration, persists. In others there are large vacuoles. In the spaces between the cells there is a quantity of granular matter derived from the breaking down of cells.

seen if the specimen is killed and fixed immediately after it has commenced to feed, that is, before the gut becomes distended with blood. The first figure on Plate XXVI shows it in a specimen of *Tabanus* removed before the completion of its first meal after hatching and fixed at once. In the section from which this drawing was made there were many places around the periphery where the layer could not be distinguished.

Secretion and excretion

The process of secretion of digestive fluid by the cells of the mid-gut in blood-sucking flies is similar to that which has been described for solid feeders. Previous to and during digestion globules appear in the protoplasm between the nucleus and the striated border, and gradually increase in size, the smaller ones coalescing to form large globules near the free border, till they distend the cell wall, causing it to bulge into the lumen of the gut. The striated border then gives way at a weak point, and a mass of globules is extruded. In many cases the orifice through which the globules pass is a narrow one, so that when the cell is killed in the act of getting rid of its contents, as in some of those in the figure, the mass is flask-shaped, and still remains attached to the cell by a narrow neck which passes through the aperture in the striated border, the remainder of the mass having rounded off as soon as it became free. In other cases the whole of the border seems to give way, and a shower of globules only loosely attached to one another is set free. During this process the cell itself alters in shape, probably on account of the state of tension which exists in its interior. The nucleus moves nearer to the lumen and the whole cell takes on a more conical shape ; it remains attached to the basal membrane by a long and narrow basal process, while the part towards the lumen is correspondingly swollen, and may project into the lumen beyond its fellows.

In some cases, but not by any means in all, the globules take with them a part of the protoplasm of the cell, including the nucleus. When this occurs the nucleus is always in a condition of degeneration, as is evidenced by the readiness and diffuseness with which it stains, and the large irregular clumps into which its chromatin is collected. Such nuclei in all stages of degeneration can be found free in the lumen in sections of the gut, and can often be seen in the act of leaving the epithelium.

In the Muscid flies one finds, in most sections, cells at all stages of this process, whether the gut is distended with blood or not ; a row of normal resting cells is seldom seen. The conditions found in the biting flies are approximately the same as in *Musca*, although their feeding habits are entirely different, as they take one large meal and then rest while digestion proceeds, while *Musca* and its allies feed intermittently. In the Orthorraphic flies, which characteristically take one large meal from the same wound, the process of excretion is seen only when the flies are caught in the act of sucking. When examined in the fasting state only globules of small size are found, and these do not cause any marked bulging of the cell. If examined after a full meal, before digestion has proceeded far, say within the first four or five hours, the cells are found to be flattened out by the distension of the gut and the stretching of the wall until they resemble a squamous epithelium; the longest axis of the cells then lies in the direction of the circular muscle fibres. Even in *Tabanus*, in which the cells are invaginated into the lumen in the form of villi in the resting condition, this is the case, as the first effect of the distension of the gut is to flatten the folds until the epithelium is disposed in a single layer of columnar cells; later, with an increase in the contents of the gut, these become flattened, gaining in one diameter what they lose in the other. The discharge of the secretion into the lumen is, therefore, a sudden one, taking place under the stimulus of the entry of blood, and is complete within a very short time after the meal is ingested. Probably the great increase in tension in the gut and its wall materially assists in the process.

The appearances seen in sections of the mid-gut during this process are to a large extent artificial. The digestive fluid contains substances which are precipitated by the alcohol used in the preparation of the tissues, and these appear in the section as granules, surrounding the clear spaces which represent the vacuoles. It is, of course, possible that some of the granules seen are pre-existent in the cell.

Digestion of blood

The action of the digestive fluid on the red blood cells results first in haemolysis, and subsequently in the formation of a brownish black pigment from the undigested residue. This occurs wherever the blood corpuscles reach the periphery, and thus come into contact with the secretion as it is discharged from the cells. But the blood in the gut is kept in a state of constant movement by the contraction of the longitudinal and circular muscle fibres of the wall, so that the layer of haemolized cells and the resulting pigment are moved away as soon as they are formed, and their place taken by fresh cells, until the whole has been digested. In some parts of the gut from which the figures on Plate XXVI were drawn layers of pigment formed in this way can be seen still retaining the impress of the depressed villi against which they were formed. At a later stage the whole of the pigment is collected in the middle of the posterior part of the chamber, being driven there by the repeated contractions of the wall. *

Contents of hind-gut

As the blood pigment increases in amount it is passed through the sphincter muscle into the hind-gut, where it mingles with the secretion of the Malpighian tubes. According to Schaudinn, the quantity of the latter, which is of a yellowish white colour, is increased as absorption of food from the mid-gut proceeds, and one should, therefore, be able to estimate the stage of digestion which exists in the gut from the colour of the faeces. The problem is complicated, however, by the fact that the hind-gut, like the mid-gut, is in a state of active peristalsis during digestion, as is shown by the frequently made observation that blood-sucking flies defaecate while feeding. The faeces first passed during the act of feeding consist of dark tarry-looking masses, which may be either the remains of the last meal, as is most probable, or freshly-formed pigment. Later fresh red blood is passed in many cases. In caught flies one almost always finds some granules of pigment in the hind-gut, in the form of small hard crystalline masses.

Regeneration of cells

As the contents of the gut are absorbed the cells lose their flattened shape; they become first cubical, and later assume their ordinary columnar form as the wall contracts around the diminishing volume of blood. Those which have degenerated and passed out into the lumen are replaced by the growth of the small cells which are always to be found between the regular columnar cells, and at their bases, in the condition of the rest. These increase in size within a few hours of the feed. In one to three days, according to the species, the temperature, and the size of the meal ingested, the gut assumes its normal appearance, and globules destined to be discharged at the next meal accumulate within the cells. When, as in *Tabanus*, the cells are heaped up into villi, these appear at an early stage, while there is still plenty of blood in the gut.

In the foregoing no account is given of the chemical aspects of the digestive process. The amount of information on this question is at present neither large enough nor sufficiently exact to be of practical use.

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* The corpuscles tend to accumulate at the posterior end of the mid-gut, and the serum at the anterior end, as a result of this peristalsis.

THE HEART, VESSELS, AND PERICARDIAL CELLS

The circulation of the blood of insects plays apparently only a secondary part in their physiology. The heart is a longitudinal dorsal tube, situated in the middle line and closely pressed against the tergal plates; it extends from the posterior part of the abdomen to the thorax, where it is replaced by a thinner vessel, the aorta, which passes through the thorax and neck, and divides into two lateral branches about the occipital foramen. The aorta and the head vessels are very hard to trace, and can as a rule only be found in the larger flies. The heart itself is best seen by dissecting off the whole of the dorsal wall of the abdomen in one piece, and then drawing two tergites apart in order to rupture the vessel. One end of it usually remains projecting from one of the fragments, and can be recognized under a low power by its pulsation.

The heart

The heart is not a simple tube, but is divided into a number of small chambers, which correspond more or less with the abdominal segments. Between each two segments of the heart there is a simple valve, which prevents the blood from flowing backwards when the walls of the chamber contract, and on each side of each segment there is an opening through which the heart is put in communication with the body cavity. There are no veins, and no arteries other than the forward prolongation of the heart referred to as the aorta.

The wall of the heart consists of a fine elastic intima, an intermediate layer of loosely arranged cells, and a muscular layer, the fibres of which are arranged as a rule in an obliquely circular direction and interlace with one another; outside these there is said to be a thin layer of fibrous tissue. The heart is separated from the rest of the body contents by a layer of muscle and membrane which constitutes a sort of diaphragm. (Plate XXVII, fig. 11.) On each side of the middle line there is a set of fine fan-shaped muscles, one pair to each tergite, which arise near the lateral borders and expand as they pass inwards; they unite with one another across the middle line as a fine sheet of membrane, which lies immediately below the heart. The space between the membrane and the insect's heart is filled in with large cells, termed the *pericardial cells*, and there are apertures in the membrane below these, through which the pericardial chamber communicates with the rest of the body cavity. The heart and pericardial cells are well supplied with tracheae; branches from all the abdominal spiracles pass directly inwards across the dorsal wall, and unite with one another in the middle line below the diaphragm.

Mechanism

The mechanism of the heart is as follows. When the muscular fibres in its wall contract, the openings by which the chambers communicate with the body cavity are closed; as the blood is compressed it passes forwards, retrogression being prevented by the valves which separate the chambers of the heart from one another. The heart is thus emptied into the aorta, and a forward flow of blood brought about.

The heart muscle then relaxes, and at the same time the alar muscle contracts; its contraction increases the space between the diaphragm and the dorsal wall, and causes the blood to enter the space through the apertures in the diaphragm, and thus to circulate among the pericardial cells in which the heart lies. Probably the muscles of the abdominal wall also assist by compressing the abdominal contents to a slight extent. Contraction of the heart then commences again, and in this way an intermittent stream of blood is kept flowing from behind forwards; all the blood circulates among the pericardial cells as it passes from the abdomen to the heart. The pericardial cells are believed to have some special function in purifying the blood, but in view of the little that is known of insect metabolism it is idle to speculate as to what this may be.

The Haematocoele

The body cavity has already been mentioned in connection with the heart, as the space from which the blood is drawn into the contractile chambers. It is worth a little more attention than is usually paid to it by parasitologists, on account of its relations to all the organs of the body, and especially to the proboscis.

When an insect is opened up by removing the dorsal or ventral wall, the internal organs are seen lying free in a space bounded only by the exo-skeleton and the layer of cells immediately internal to it; they have no attachments other than those formed by the tracheae. This space is the haematocoele. In the living insect it is filled up by the blood, which bathes all the internal structures and is kept moving by the action of the heart. The stream of blood passes forwards in the dorsal tube, and, leaving it at the termination of the aorta in the head, it returns to the abdomen in two lateral streams, which divide up into numerous streamlets as they pass among the contents of the cavity. Now the lumen of the alimentary tract is only separated from the blood in the haematocoele by the thickness of the wall, and this is neither very great nor is the wall in that part which lies in the thorax and abdomen of such a nature as would render it difficult of penetration by any parasite possessed of means of movement. Once a parasite has penetrated the wall of the alimentary canal and become free in the body cavity, then, whether it is motile or not, it will, unless it is too large to pass through the lateral openings into the heart, be drawn into the circulation and transported to the head ; it may then, of course, find its way back in the slower backward stream, or it may become attached or entangled in some part of the body.

The relations of the haematocoele in the proboscis of the fly have been described at some length in connection with the mechanism of the mouth parts. If what was said on that subject be considered from the point of view of the possible movements of a parasite which has perforated the wall of the alimentary tract, it will at once be obvious how intimate are the relations of the parasite to the blood in the wound, or to the food surface in the case of the non-biting flies. Once it is free in the blood of the abdomen it may be caught up at the dilatation of the heart, and on the next contraction it may be forced along with the blood stream into the aorta, and so on directly to the head. In the eversion and closure of the labella, which together constitute the act of biting in the Muscid flies, there is a forcible and rapid to-and-fro movement of the blood in the lower part of the proboscis, and the chances that the parasite will sooner or later be driven into the space between the inner and outer walls of the labella are very great indeed. When it has arrived there it is only separated from the blood of the presumptive vertebrate host by the thin inner wall of the labella. Whether and under what circumstances this inner wall could be perforated is one of the questions to be decided in each case.

The relations of the haematocoele of the labella are the most striking in the case of *Musca* and its biting allies, but the same conditions are to be found in the Orthorraphic biting flies. The labella of *Tabanus*, when they function as feeding organs, are distended in exactly the same way as those of *Musca*, and the distension can be readily demonstrated experimentally by pressure on the head. In other forms, in which the labella are not functional in this manner, it is extremely probable that something of the same kind occurs in the eversion of the labella preliminary to the insertion of the piercing parts. In the mosquito the position of the tip of the proboscis, which appears to act merely as a guide and support to the other parts, is a most suggestive one.

The blood is easily obtained for examination by taking one of

PLATE XXVII

Figure 1. The nervous system of *Tabanus*. br., brain. a.n., antennal nerve. o.l., optic lobe. n.t., nerve trunk, formed from two branches which emerge from the suboesophageal ganglion. t.g., thoracic ganglion. ab.g., abdominal ganglia. × 140.

Figure 2. Pericardial cells from *Haematopota*. × 500.

Figure 3. Fat body from a newly hatched *Philaematomyia*. eo., compact homogeneous particles which stain brightly with eosin. v., vacuoles. n., nucleus.

Figure 4. The compound thoracic ganglion of *Musca domestica*. After Gordon Hewitt.

Figure 5. Cross-section of the salivary gland of *Haematopota*. × 400.

Figure 6. Longitudinal section through the salivary gland of *Culex*. sl.d., the salivary duct. × 800.

Figure 7. The salivary gland of *Culex fatigans*.

Figure 8. The salivary gland of *Anopheles rossii*.

Figure 9. One salivary gland of *Tabanus albimedius*. × 30.

Figure 10. Cells of the labial salivary gland of *Haematopota*. These are similar to those in *Musca*, and to those of *Philaematomyia*, in which, however, the permanent vacuole is not so well seen. n., large nucleus. n′., small nucleus at the opposite end of the cell. v., vacuole. × 650.

Figure 11. Scheme of the circulatory system. h., heart. p.c., pericardial cell. t., tergite. al.m., alary muscle: the tendons spread out in the middle line, and form a wide sheet perforated in places. ha., haematocoele. ov., ovaries. al.t., alimentary tract. st. sternite. The arrows indicate the direction of the flow of the blood, through the interstices between the fat body and the organs, into the pericardial chamber and the heart, within which it is propelled forwards through the aorta to the head.

PLATE. XXVII.

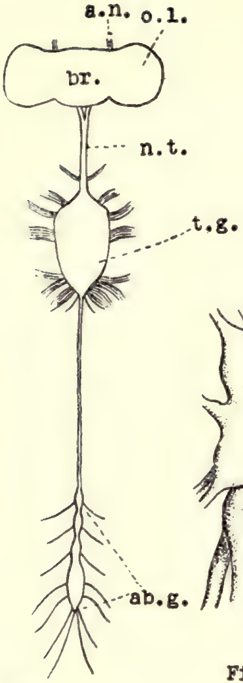
a.n.
o.l.
br.
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Fig. 1.

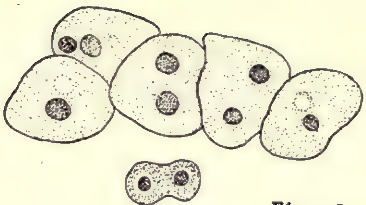


Fig. 2.

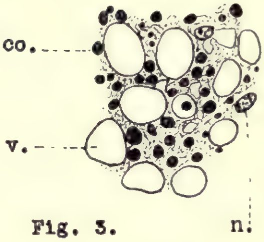


Fig. 3.

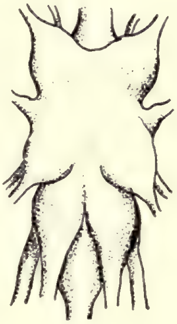


Fig. 4.

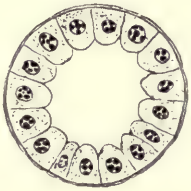


Fig. 5.

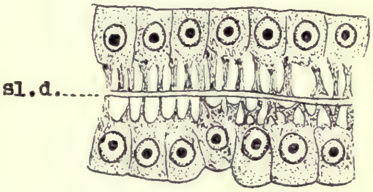
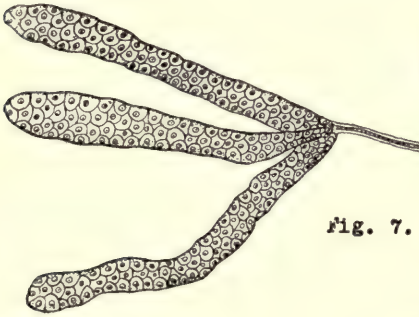


Fig. 6.



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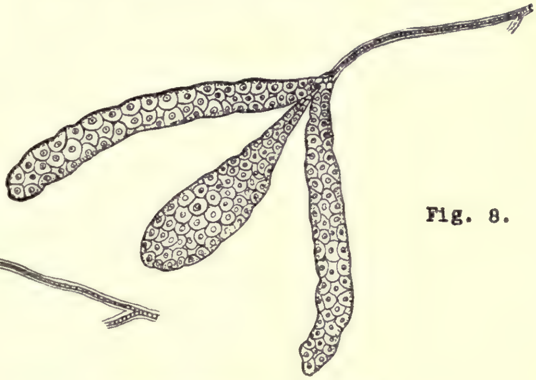


Fig. 8.

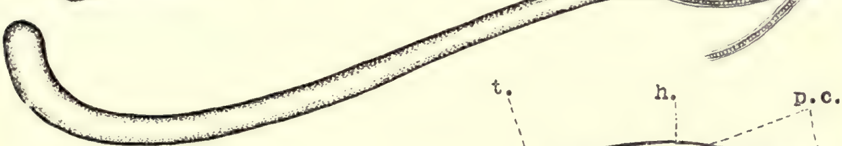


Fig. 9.

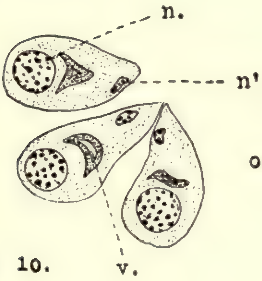


Fig. 10.

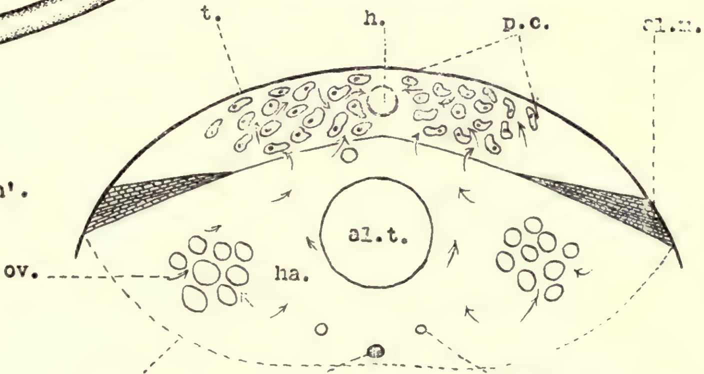

t.
h.
p.c.
cl.m.
ov.
ha.
al.t.
st.
n.
mp.t.

Fig. 11.

the larger flies, and, without other dissection, making a small nick in the membrane connecting two of the abdominal plates. A pipette with a fine bore is then inserted, and a considerable quantity of a yellowish fluid obtained. Blood may also be obtained in small drops, but with more risk of contamination, by pulling off the legs and picking up the fluid as it escapes on a cover-slip; or in the case of flies with a well-developed pseudotracheal membrane, by compressing the head until the blood is pressed into the labella, from which it can be withdrawn in a pipette, or smeared out by rupturing the labella on a slide.

The blood

Blood so obtained is a rather viscid yellow fluid, containing an extremely small number of cells; so poor is the fluid in cellular contents that several large smears may have to be examined before finding a single cell, and those which are seen may be so fragmentary and indistinct as to be hardly recognizable as such. Many varieties of cells have been described from insect blood, but when special precautions are taken to avoid touching any of the internal organs one frequently finds no cells at all, or at most a few which might be the small hypodermal cells internal to the integument. The blood corpuscles, sometimes called leucocytes (the *amebocetti* of Berlese), are very small rounded or oval bodies, each containing a single nucleus and a reticulated cytoplasm. In many a definite nucleus is absent.

The fat body

On opening the abdomen of a recently-hatched insect all that is seen at first is a sheet of whitish tissue, with a greenish or bluish tinge, which envelopes all the organs. When this is split up by dissection it is found to consist of a number of minute lobules connected together by thinner portions, which are drawn into threads as they are pulled on by the needle. This is the so-called fat body, really a mass of only slightly differentiated mesoblastic tissue, the walls, if such they may be called, of the haematocoele. It envelopes all the internal organs, and is always found in considerable quantity around the digestive part of the alimentary tract; a thinner sheet of it forms an inner coating to the internal surface of the body wall; between these two layers, and in all the interstices between the lobules and the cells of which the tissue is composed, the blood of the fly passes as it circulates to-and-fro in the body. The cells of the fat body are large, and when closely packed together are moulded to one another so as to present a mosaic pattern on section; in newly-hatched flies they contain a nucleus and a finely-reticulated protoplasm, and are loaded with globules of fat (Plate XXVII, fig. 3).

The exact function of the fat body is not known, but it is evidently an important one closely connected with the metabolism of the fly, for it has a rich supply of tracheae. The quantity present in newly-hatched flies and in fully-fed larvae is much greater than that found in older specimens, and the appearance of the cells is greatly altered concurrently with the diminution in amount. The cells lose their nuclei, the protoplasm becomes broken up and replaced by large vacuoles, and sometimes crystals may be found in them. Most probably the fat body is a store of reserve food material accumulated in the larval stage, to assist the insect in the reproductive phase; there is also some reason to believe that it assists in the elimination from the body of waste products.

THE REPRODUCTIVE SYSTEM

The organs of reproduction are situated in the posterior part of the abdomen between the alimentary tract and the ventral chain of nerve ganglia. The external opening lies anterior and ventral to the anus, from which it is separated by the sternal plate of the last segment. The separate elements of which the system is composed are paired and situated laterally, only the posterior efferent duct and the opening to the exterior being common to the two sides. The genital opening is surrounded by certain modified parts of the exo-skeleton, forming the external genitalia already described, the purpose of which is to assist in copulation, and, in the female, in oviposition. The sexes are always complete and distinct from one another in the Diptera. The internal organs of reproduction of the male exhibit a wide degree of variation, as is the case with the external parts.

General structure

The essential sexual elements are certain cells derived from the blastoderm, which are contained in the male *testes* and in the female *ovaries*. Leading from these organs there are ducts to convey the sexual products to the exterior, known as the *vasa deferentia* and the *oviducts* respectively; in the course of these ducts there may be dilatations or diverticula for the reception of the sperms, prior to copulation in the male, and after copulation in the female. The posterior portions of these ducts are fused with one another, and are formed, together with a portion of the bilateral ducts, by an invagination of the cuticle; they are therefore lined with chitin continuous with that of the exo-skeleton. The chitin may be present in a dense and pigmented layer in certain parts, as in the spermathecae of mosquitoes. In association with the system there are usually certain glands of a mucous nature and of considerable size; those of the female are designed to provide the ova with a superficial covering, by which they are in many cases attached either to one another or to some stationary object. The external opening of the male tract is at the end of a chitinous *penis;* that of the female is a dilatable chamber with a muscular wall. The fused portion of the female tract may become very highly developed in the pupiparous forms, in which it contains the larva during the period of its growth and development.

Relations of sexes

Much yet remains to be investigated regarding the relations of the sexes in the Diptera. It has been said that the spermathecae, or the dilatations on the efferent duct of the tract in the female, contain the spermatozoa derived from the male. The female, once having received a supply, can go on developing her ova in several batches, without being dependent, so far as is known, on a second copulation. But it is not known with certainty at what period of the growth of the ova fertilization takes place, or how soon after emergence from the pupal state the two sexes meet. There appears to be some relation between the time at which the first feed is taken and the time at which copulation occurs, which may perhaps account for the extraordinary difficulty which is sometimes met with in persuading newly-hatched flies to feed. There also remains to be explained the well-known difference which is found in the proportions of the two sexes. When breeding mosquitoes, for instance, a large majority of those which emerge are males, while on the contrary there are some species of *Tabanus* and *Haematopota* of which the female is a common fly, and the male extremely rare. The difference in numbers in the latter case is far too great to be accounted for by the more obtrusive habits of the female. The conditions suggest that the male, once having copulated and fulfilled its purpose in the propagation of the race, dies off, leaving the female to live as long as she has eggs to lay. The point may possibly have a practical interest in cases in which both sexes are blood-suckers.

The Male Organs

The male organs are confined to the posterior portion of the abdomen, and are only of interest here in that the observer should be able to recognize them when met with during dissection.

Culex and Tabanus

In the mosquito (Plate XXVIII, fig. 3) the testes are small ovoid bodies, with a slightly green tinge in the fresh state. The vasa deferentia which lead from them are extremely slender tubes of considerable length; each expands at the distal end to form a small receptacle, from which a short common ejaculatory duct passes to the genital opening. On each side there is a globular accessory gland closely pressed against the seminal receptacle. In *Tabanus* (fig. 1) the testes are similar but a little longer, and have much shorter vasa deferentia, which open into a seminal receptacle of considerable size ; the receptacle is pear-shaped, and receives the vasae at its broad anterior end ; it opens below by an ejaculatory duct into the chitinous penis. It has much muscular tissue in its wall, and presumably plays an active part in expelling the seminal fluid in copulation.

Phlebotomus

In *Phlebotomus*, the parts of which have been described by Newstead and Grassi, the testes are small oval organs of variable outline, which lead by short ducts to a pear-shaped seminal vesicle, which in turn is produced into a short ejaculatory duct. This leads to an interesting apparatus termed by Grassi the 'pompetta'; this consists of a hollow cylindrical chamber containing a piston-like rod, which is provided with muscles by means of which it can be moved up and down ; as the opening of the ejaculatory duct is near the lower end of the chamber, the action of the rod will be, according to Grassi, to regulate the exit of the seminal fluid after the manner of a pump.

Musca

In *Musca* and its allies (fig. 4) the testes are recognized at once by their brown colour. They are small pyriform bodies, leading by a short and narrow vas deferens to a stouter common duct, which may be regarded as the vesicula seminalis. Its lower end is contracted to form a short ejaculatory duct. There are no accessory glands.

Glossina

In *Glossina* the reproductive organs of the male are different to those of the rest of the Muscidae, and resemble rather the type found in the Pupipara. The testes are simple tubes of a brownish colour and are twisted on themselves in many coils. The testicular tube is continued downwards to become continuous with a vas deferens of slightly greater calibre. These unite in the middle line to form a common ejaculatory duct. There is a pair of accessory glands, twisted on themselves like the testes, but distinguished from them by their white colour and by the fact that they do not terminate in a fine point as do the latter. These open at the point of fusion of the vasae to form the ejaculatory duct.

Hippobosca

In *Hippobosca* (fig. 4) the testes are simple tubes of very great length, and are twisted on themselves to form a compact mass like a ball of string. The terminal portion is a little wider than the rest, and is usually to be seen on the outer side, slightly separat-

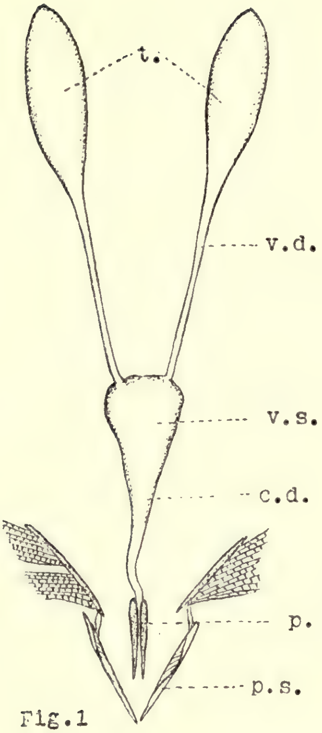
PLATE XXVIII

Figure 1. The genital organs of *Tabanus*, ♂. × 20.
Figure 2. The genital organs of *Musca*, ♂.
Figure 3. The genital organs of *Culex*, ♂. × 50.
Figure 4. The genital organs of *Hippobosca*, ♂. They resemble those of *Glossina*. × 90.

Reference letters

t.	testes.
v.d.	vasa deferentia.
c.d.	the common ejaculatory duct.
v.s.	vesicula seminalis.
a.g.	accessory glands.
p.	penis.
p.s.	sheath of the penis.
t′.	in figure 4, the terminal portion of the testicular tube.

PLATE XXVIII.


t.
v.d.
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p.s.

Fig.1

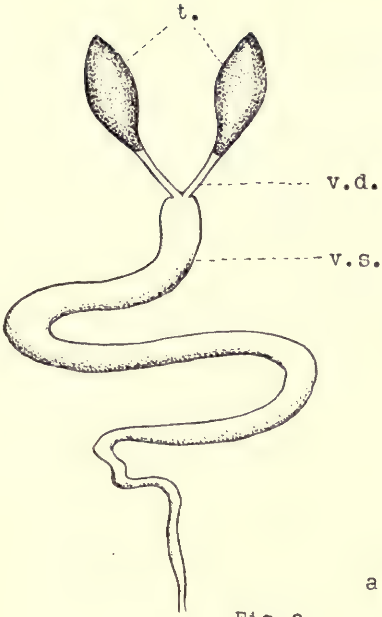

Fig.2

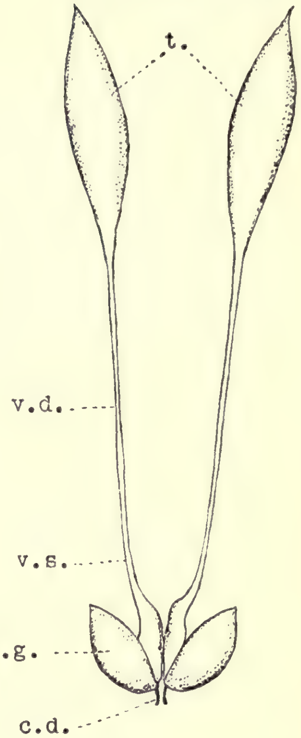

Fig.3

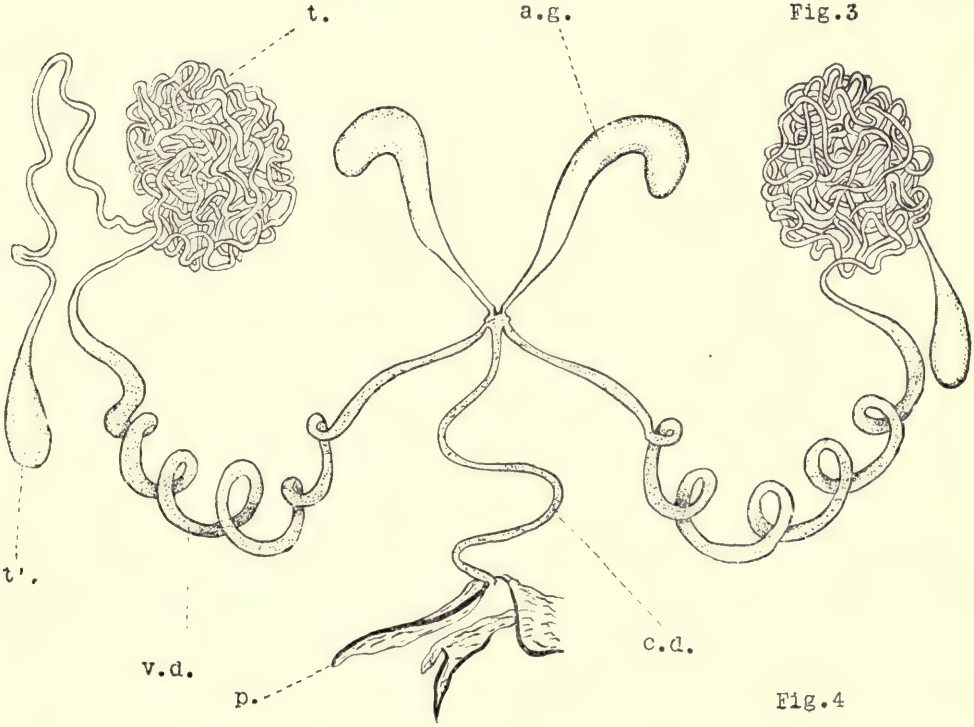

Fig.4

ed from the coil. The lowest coil of the tube is continuous with the vas deferens, which is also twisted, but more loosely. The two vasae meet in the middle line, as in *Glossina*, to form a common ejaculatory duct, which is of much thinner calibre. Both the vasae and the testicles are of a rich brown colour. There is a pair of accessory glands, not coiled, but dilated and bent at the upper end, which open at the junction of the vasae of the two sides. These accessory glands are of a glistening white colour in the fresh state. There are two pairs of such glands in *Melophagus*.

The reproductive organs of the female are of special interest in connection with the hereditary transmission of parasites.

The Female Organs

Reproduction among the Diptera takes place, in the majority of instances, by the deposition of eggs and a complete metamorphosis. In some, however, the development from egg to larva takes place in the body of the female, and the larva is produced either when still young and active or when it is ready for pupation. The oviparous forms will be discussed first.

The essential organs of the female are the ovaries, each of which consists of a number of *ovarian tubes*, or *ovarioles*. The ovarioles open into an ovarian duct on each side, the ducts of the two sides uniting to form a common channel. This in turn leads into a short cavity known as the *bursa copulatrix*, which opens at the genital opening. The *spermathecae*, or receptacles for the sperms from the male, and the accessory glands, open into the *common oviduct*. It is the common oviduct which is modified to form a receptacle for the larva when it passes through the whole or a part of its development in the body of the parent.

Ovaries

The *ovaries* are rounded or pear-shaped bodies possessing little cohesion or definite shape. The separate tubes of which they are composed are only very loosely attached to one another, the investment of the whole organ consisting of a few scattered muscular fibres continued upwards from the oviduct. Each ovarian tube terminates as a fine filament at the upper end, and the filaments from each tube in the ovary are collected together to form a sort of suspensory ligament, which passes upwards and forwards, and can be traced to the fat body in the region of the heart. This is known as the *apical filament*.

The size and shape of the ovaries depend entirely on the condition of the eggs which are developing in them. When the batch of eggs to be laid next is approaching maturity, the ovaries are very large, and may compress all the other abdominal contents into the anterior and dorsal portion of the cavity, at the same time distending the abdominal wall and stretching the membrane which unites the dorsal and ventral plates. The mature ovaries of the mosquito appear as conspicuous white bodies, easily seen through the ventral and lateral walls of the abdomen. In newly-hatched females, on the other hand, the ovaries are very small and inconspicuous.

Each ovarian tube is divided into a number of chambers or follicles, each of which produces one egg. There are usually four or five follicles to be seen in each tube, and these show a progressively advanced stage of development from the apical filament downwards, the uppermost one consisting only of a small collection of undifferentiated cells, while the lowest follicle contains a well developed ovum. When one batch of eggs is laid the next lowest follicle comes to maturity and takes its place, and so on in rotation during the life of the fly.

Structure of follicles

The structure of the follicles is best explained by following the development from its early stages. In the newly-hatched fly they are very small and delicate structures, consisting only of a number of large cells at the upper end of the ovarian tube. Out of this mass three different parts arise. The central cells enlarge, and one of them, the future *ovum*, passes to the lower part of the mass; the rest, which are to become the *nurse cells* whose duty it is to nourish the ovum, pass to the upper pole. The remainder become changed into a layer of regular cubical cells, which form a covering for the ovum and its nurse cells. A number of cells from the original mass remain at the upper pole, outside the epithelial layer. The ovum and the nurse cells now begin to show marked alterations. The nurse cells become greatly enlarged, and have very large nuclei, while the ovum accumulates around its nucleus a quantity of granular material, which, gradually increasing in amount, forces the nurse cells still further towards the upper pole, until the ovum comes to occupy the greater part of the space in the follicle. The epithelium remains as a complete layer covering the whole. The granular food material of the ovum soon obscures the nucleus, so that it can no longer be made out in fresh preparations. When the egg is ripe the epithelial layer forms a part of its covering, while the nurse cells disappear entirely.

While this is going on the small mass of cells left outside the first follicle also commences to undergo a similar series of changes, but as it starts after the first follicle it is always smaller. It in turn

PLATE.XXIX.

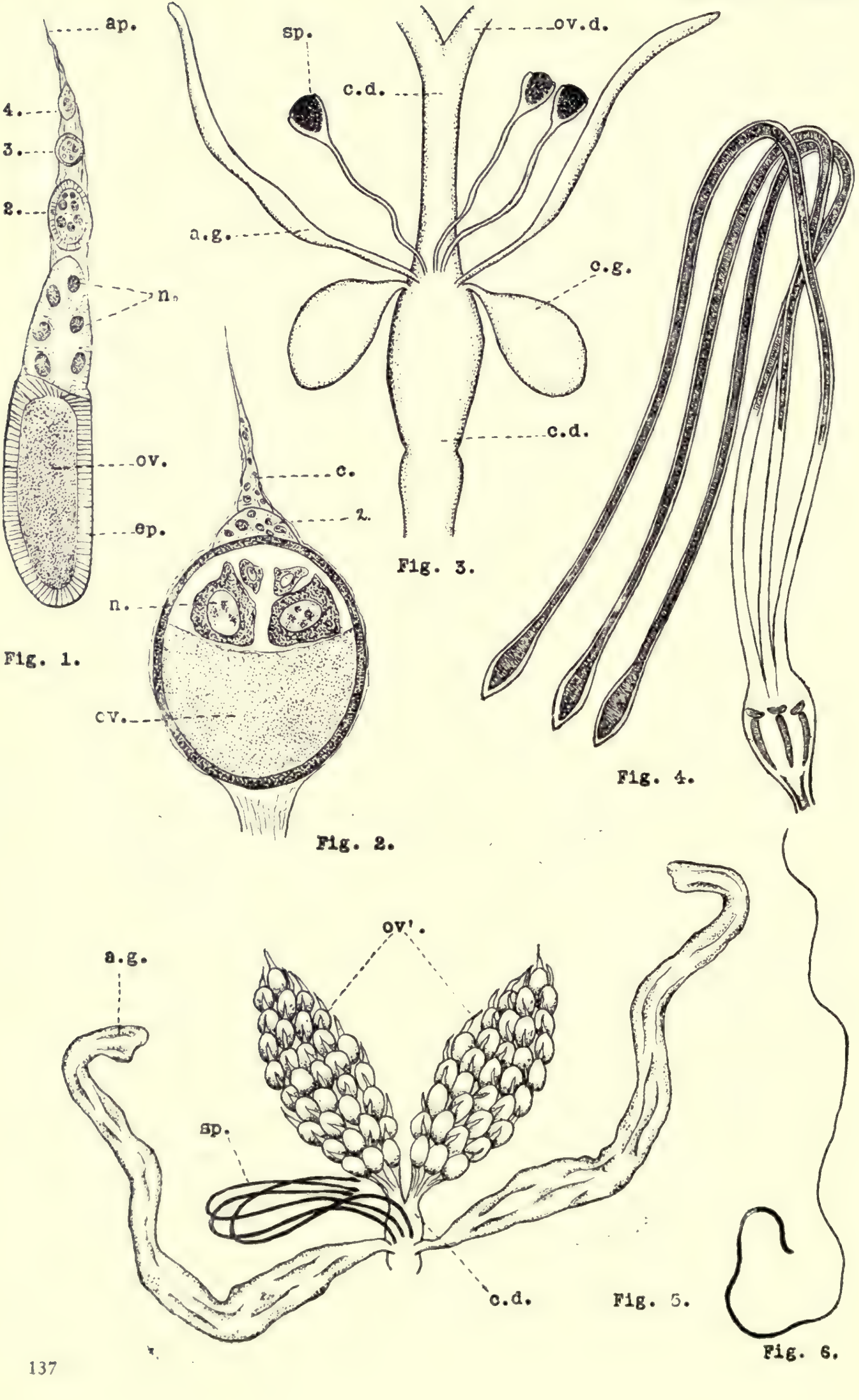
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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

PLATE XXIX

Figure 1. An ovarian tube from *Stomoxys*. × 50.
Figure 2. An ovarian tube from *Culex*. × 350.
Figure 3. The common oviduct and connected structures of *Musca*.
Figure 4. Spermathecæ of *Haematopota*. × 32.
Figure 5. The reproductive organs of *Haematopota*. × 12.
Figure 6. Spermatozoon from *Musca nebulo*.

Reference letters

ap.	apical filament.
2, 3, 4	undeveloped follicles.
n.	nurse cells.
ov.	ovum.
ep.	epithelial layer.
sp.	spermathecæ.
a.g.	accessory glands.
c.d.	common ovarian duct.
ov.d.	oviduct.
c.g.	conglobate gland.
c.	mass of undifferentiated cells, in which separate follicles cannot be distinguished (germarium).

has a small cap of undifferentiated cells at its upper pole, which goes to form the third follicle, and so on, the succeeding follicles being progressively smaller in accordance with their age. In the mature ovariole there is, therefore, one fully developed egg ready to be laid, and several follicles at various stages of growth.

The above account will apply to the Diptera generally. Individual differences are found in the relative degrees of development at which it is usual to find the different series of eggs, and this affects the shape of the ovarian tube as a whole. In the mosquitoes the first follicle becomes nearly mature before the development in the second is much advanced, and while the third and fourth are little more than masses of undifferentiated cells; when the apical filament is broken and the tube rendered flaccid these undeveloped follicles appear as a little cap on the upper pole of the nearly mature egg. In the Muscidae the follicles after the first are more advanced, so that an isolated tube appears longer. *Tabanus* occupies an intermediate position. In each case, however, the appearance is accentuated by the shape of the egg; that of *Culex* (Plate XXIX, fig. 2) is almost round, while that of *Stomoxys* (fig. 1) is a long ovoid.

Oviducts

The paired oviducts and the common oviduct have muscular walls with well developed transverse fibres, which doubtless aid in the expulsion of the ova. They are lined internally with a layer of flat cells with small nuclei, superficial to which there is a delicate lamina of chitin continuous with that of the integument. The bursa copulatrix is not as well developed in the Diptera as it is in some other orders of insects, and is not easily distinguished. In *Haematopota* it is provided with a series of minute spines set on a chitinous framework, which apparently engage with the male organs in copulation.

Spermathecae

The other parts of the reproductive system show considerable variations in the different genera. The spermathecae are small chambers with chitinous and pigmented walls, formed as invaginations of the wall of the oviduct, and having, therefore, a layer of small cells external to the thick chitinous wall. In *Anopheles* there is only one such sac, with a long and narrow duct. In *Culex* and *Stegomyia* there are three. In *Tabanus* and *Haematopota* (fig. 4) the spermathecae are long fine tubes, bent on themselves in the middle of their length; the slightly expanded blind ends are attached to the wall of the oviduct near the origin of the tube. The chitin forming the internal layer of the wall is thickest near the blind end, and is transversely striated. At the base of each tube, where it joins the oviduct, there is a peculiar funnel-shaped collar of thick chitin, surrounded by a series of spiral filaments like the rings of a trachea. The whole tube has a distinct coating of muscle fibres. In *Phlebotomus* there are only two spermathecae, one on each side of the middle line at the junction of the oviducts. They are relatively large and thin walled, but at the point where the duct leaves them the wall is thicker, and is thrown into transverse ridges. In *Musca* (fig. 3) there are three spermathecae resembling those of the mosquito, but flattened at the top, and without a continuous chitinous wall.

Accessory glands

The accessory glands differ in size. In *Anopheles* they are very small, and open near the lower end of the oviduct. In *Tabanus* (fig. 5) they are large, and are conspicuous in dissections on account of the dirty yellow colour of the secretion which they contain. The wall is composed of columnar epithelial cells with many muscular fibres, and is thrown into longitudinal folds. In *Phlebotomus* also there is a pair of long tubular glands. In *Musca* (fig. 3) there are two pairs, one long and thin, and another, the so-called *conglobate gland*, rounded or pear-shaped; the latter is situated close to the wall of the oviduct, and is often difficult to see on that account.

The Reproductive Organs in the Pupiparous Flies

The pupiparous habit occurs in three distinct degrees in the Diptera. In many Tachinids, which are not blood-suckers, the larvae are delivered almost as soon as they hatch out of the egg, and are very small. They undergo little or no development in the uterus, and are laid in a large batch, exactly as eggs are laid. If the ovaries are dissected out just previous to oviposition the young larvae can be seen within the egg membranes; they are perfectly formed and show active movements, as if they were trying to find a way out of the egg. In the next degree, which is instanced by two species of *Musca*, namely, *corvina*, Fabr., var. *vivipara* Portschinski, and *bezzii*, Patton and Cragg, which are both blood-feeders, the larva is retained and nourished for a part of its life in the genital tract of the female, but is deposited while still young, and completes its growth under conditions similar to those of its allies. In the third degree the larva is retained until it is ready to pupate, and in consequence of its large size during the later stages the genital tract is greatly altered in its shape and relations. Glands are also developed to provide nourishment for the growing larva.

As the Tachinidae are not blood-feeders they need not be discussed

Origin of pupiparous habit

here. Their peculiar method of reproduction is the outcome of the circumstances under which the larval stage is passed, for these flies deposit their eggs, or young larvae just hatched from the eggs, in the bodies of other larger larvae, usually those of Lepidoptera, and a reduction of the immature stages is a necessary condition of their existence. The larval stage must be completed before the host pupates, or immediately after, lest the food supply should be exhausted. In the other two cases there is no such apparent necessity for an acceleration of the stages, and we must look elsewhere for an explanation of the origin of the habit. Probably two factors enter into it. In the first place, the larva while retained in the body of the active female will avoid a large proportion of the dangers to which a free larva is subjected, both from predaceous insects and from birds, and from accidental conditions such as loss of food supply, exposure to adverse conditions of temperature and moisture, etc. A larva which only leaves the body of the female when it is ready to protect itself by pupation has obviously a better change of reaching the mature stage than one which has to live free for a considerable period. Secondly, the rich supply of food which blood-sucking insects can obtain appears to have some relation to the pupiparous habit. Although the number of Diptera which feed on blood is exceedingly small in proportion to the size of the order, the number of pupiparous forms is very high, including the whole group known as the Pupipara, the genus *Glossina*, and some Muscids. Even in *Philaematomyia insignis* a shortening of the first stage can be noticed, for the eggs are much larger when laid than one would expect for the size of the fly, and the larvae hatch from them at a much earlier period than the larvae of other Muscids under identical conditions. The subject is a very obscure one, but the association of the blood-sucking habit with the pupiparous habit is clear enough, and one should always be on the look out for larviparous forms among those known to suck blood, whether they are biting flies or not.

The term 'pupiparous' is really a misnomer, for the instar which is produced from the mature female is a full-grown larva, which does not pupate until it is in suitable surroundings. The larva of *Glossina* when born is able to move about until it finds a suitable place for pupation. That of *Hippobosca* is not motile, but passes into the pupal stage at the place where it leaves the female.

Musca bezzii is an example of the second degree, in which a young larva is produced. In the early part of its life the larva is nourished by the mother, while in its later stages it obtains food for itself after the manner of its kind. *Musca corvina* (var. *vivipara*) appears to have a similar life history; in all probability the habit is by no means a rare one.

Musca bezzii

In *Musca bezzii* there are only two ovarioles, each constituting the ovary of its own side. As in the other Muscids, the ovariole is divided into a number of follicles, in each of which there is an ovum, more or less mature. But as only one larva can be contained in the uterus at one time, the ova in the two tubes are never in the same state of development, the lowest one of one side being always more advanced than that of the other. The upper follicles, also, are not stretched out in line with the first, but are bent over and appear to be attached to the side of the large lowest follicle containing the mature or nearly mature egg. This is a result, partly at least, of the alteration in the position of the parts of the reproductive organs in consequence of the presence of the larva, which thrusts the ovaries forward and to the dorsal side as it grows. The two ovarioles distal to the last follicle are continued downwards as oviducts, which unite in the ordinary manner to form a common oviduct, which leads in turn to the genital opening. The walls of both the paired and unpaired oviducts are very well supplied with muscular fibres, which are arranged in definite transverse and longitudinal bands. The transverse bands are very well developed at the distal end, and form a sort of sphincter around the genital orifice.

The appearance and relations of the common oviduct, which may be termed here the uterus, differ entirely according to the contents. When it is empty it forms a simple elongate and rather spindle-shaped chamber, resembling that of the oviparous species of *Musca*, but of greater length. But when it contains a larva ready for birth it is enormously increased in size, and is pressed forward into the anterior and ventral region of the abdomen; its upper end, at which the mouth of the larva is situated, is expanded beyond the point at which the paired ducts unite, so that the latter appear to join the uterus some distance behind the anterior end. The whole chamber is bent a little in accordance with the attitude of the larva, which does not lie stretched out in a straight line, but is arched so that its lower border is concave.

When the uterus is empty it is usual to find a nearly mature egg in one of the follicles, and, *vice versa*, when the uterus contains a growing larva the ripest egg is still immature. The two ovarioles function alternately, first one and then the other producing a ripe ovum and passing it into the uterus.

The stay of the larva in the uterus is not a long one, and there is no elaborate arrangement of milk glands, such as is found in the true Pupipara, for the nourishment of the growing young. There is a single pair of accessory glands, which open at the upper end of the common oviduct; these are certainly much larger than those found in the oviparous forms.

The spermathecae resemble those of *Musca*, two of them, however, being inserted by a common duct. All three ducts are very much coiled.

The following account of the female reproductive tract of *Glossina* is taken from Roubaud. The writers have not had the opportunity of examining *Glossina* in the fresh state.

Glossina

The apparatus consists of two parts, the ovaries and their accessory organs (spermathecae and milk glands), and the unpaired portion, the oviduct, uterus, vagina, and the common duct of the milk glands.

Ovaries

The *ovaries* are of the same type as those of *Musca bezzii.* There is one ovariole on each side, containing at most four or five follicles, and the two sides function alternately, first one and then the other producing a mature egg in the lowest follicle. As in *bezzii*, the upper follicles are so much outgrown by the lowest one that they appear to be attached to its lateral aspect. Each ovarian tube opens by a short canal into the median unpaired oviduct, which in turn opens, after a slight dilatation, into the upper end of the uterus. The walls of the ovarian tube are composed of an external layer of muscle fibre, and an internal fibrous layer adherent to this.

Uterus

The *uterus* is a large distensible sac, the dimensions of which necessarily vary according to the state of the development of the larva; when the larva has attained to full growth it occupies almost the entire ventral region of the abdomen. It is held in position by a rich tracheal network, best developed on the ventral surface and at the sides, and by various muscles, the arrangement of which has been described by Minchin. The disposition of these is sufficiently indicated in the figure (Plate XXX); in addition to those shown there is a large unpaired muscle in the middle ventral line which connects the uterus with the ventral abdominal wall. These muscles support the heavy uterus during gestation and are able to adjust its position in the abdominal cavity.

The walls of the uterus are composed of an external tunic of muscle fibres, arranged in longitudinal, circular and oblique bands, and a fine chitinous lamina on the internal aspect. The oviduct, which leaves the organ on the dorsal side of the upper end, is of a similar structure. Immediately behind the entry of the oviduct into the uterus there is a conical elevation of the wall, on the top of which are situated the orifices of the ducts of the spermathecae and nourishing glands. At this point the chitinous and muscular layers of the wall are greatly increased in thickness.

The posterior contracted portion of the uterus forms the *vagina*. It has a structure similar to that of the uterus, the chitinous lamina of the wall being, however, increased in thickness. It is provided with dilator muscles by means of which the cavity can be widened at the moment of the birth of the larva.

Spermathecae

The *spermathecae* are small rounded spheres of a yellow colour, the tint being due to the thick chitinous lamina which forms their internal wall. External to the chitinous layer, which in *palpalis* and *tachinoides* is adorned with small raised areas on the internal surface, there is an investment of a single layer of highly-vacuolated cells. In *G. fusca* the raised areas are absent, and the outer investment consists of two layers of non-vacuolated cells.

The two spermathecae are united in a common cellular investment, and open, each by a fine canal, into the dorsal aspect of the uterus. The inner walls of these ducts show an arrangement of chitinous spirals like those of a tracheal tube, but with the rings more separated and less numerous. The external cellular covering is thin and the cells are without vacuoles. The two ducts open into the uterus at the same point, and here the circular muscle fibres are arranged to form a sphincter.

After fertilization the cavity of the spermatheca and its duct is filled with spermatozoa, which are also found within the cavity of the uterus at the level at which the ducts open. This is also the point at which the mouth of the larva is situated during gestation, and one might suppose, Roubaud remarks, that the spermatozoa which are not used up in fertilization are absorbed by the larva, as has been stated by Berlese to occur in *Melophagus*, along with the secretion of the nutrient glands.

Milk glands

The nutrient glands, or *milk glands*, are characteristic of the genital apparatus of the pupiparous Diptera. In *Glossina* they are much branched tubular glands, which are situated dorsally on each side of the uterus and open into its cavity by a common duct just behind the opening of the ducts of the spermathecae. The dimensions and the amount of ramification of the glands depend

PLATE XXX

Figure 1. Genital apparatus of *Glossina palpalis*, ♀, dorsal view, after Roubaud.
O., the oldest egg. o'., nurse cells of the second follicle. Od., oviduct. Od. C., common oviduct. Sp., spermathecæ. C. Sp., their duct. Gl., uterine glands. C. gl., their common excretory duct. Ut., uterus. V. vagina. M.r., retractor muscles of the uterus. M.p.d., M.p.v., dorsal and ventral protractors of the uterus. M.d., Dilator muscles of the vagina. The figures 1. 2, 3, . . . 8 represent the relative age and order of succession of the different ovules.

Figure 2. The genital apparatus of *Musca bezzii*, ♀. a.g., accessory gland. Other letters as before. × 10.

Figure 3. The genital tract of *Melophagus ovinus*, ♀, dissected from the body, and seen from the dorsal side. After Pratt. × 33. med. ovi., median oviduct. pa. ovi., paired oviduct. rec. sem., receptaculum seminis. a.m.gl., anterior milk glands. ov., ovary. p.m.gl., posterior milk glands. U., uterus. vag., vagina.

Figure 4. Longitudinal section of the two ovaries, the paired oviducts, and the receptaculum seminis, of *Melophagus ovinus*. ovar. 1., ovar. 2., the two ovarioles of each ovary. 1, 2, 3, . . . 8, the different follicles in the order in which they discharge their ova. n.ce., nutritive (nurse) cells. ger., germarium. After Pratt. × 52. (reduced from original.)

PLATE XXX.

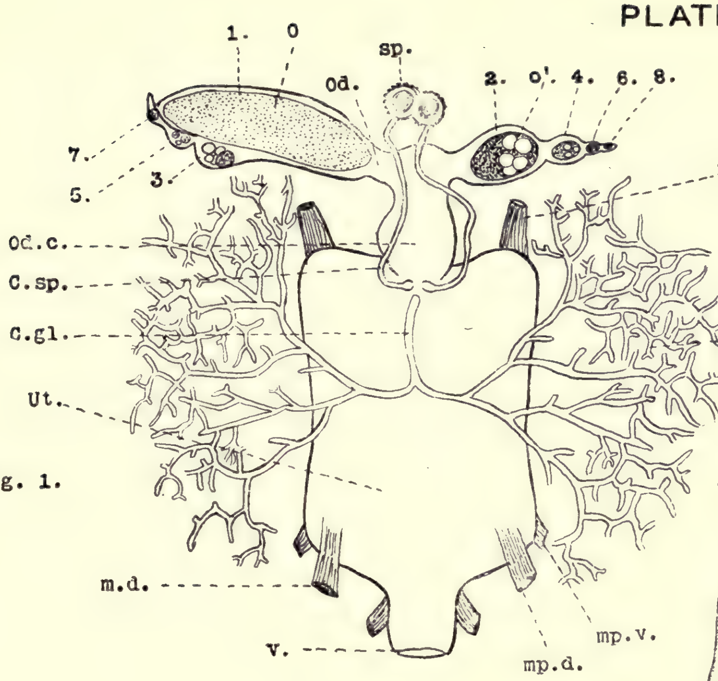
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Fig. 1.

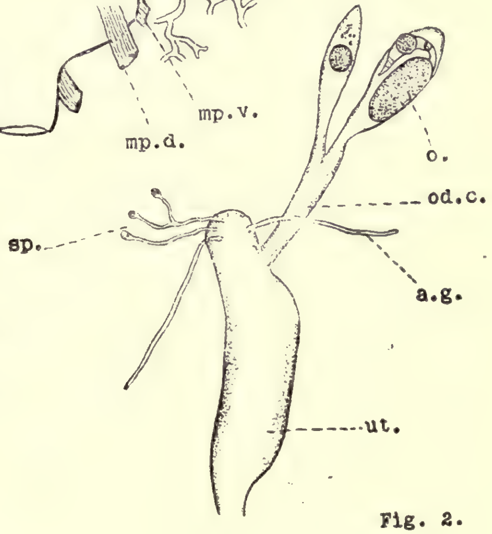
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Fig. 2.

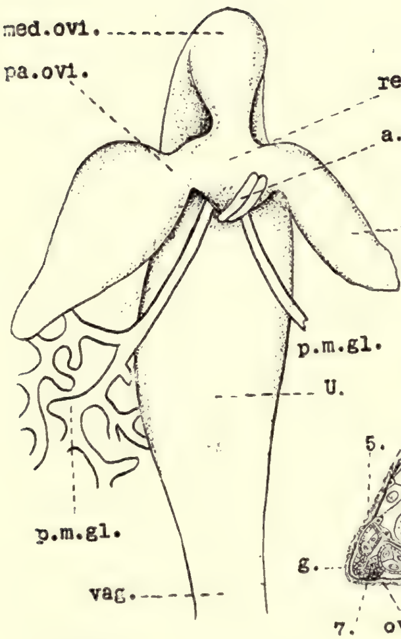
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Fig. 3.

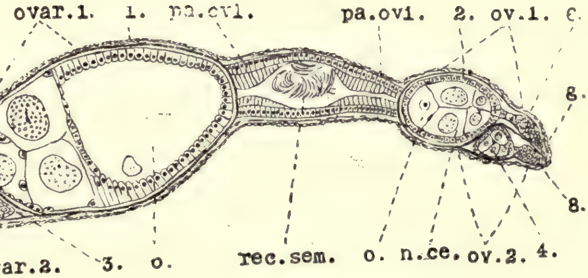
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Fig. 4.

upon the age of the fly and stage of the reproductive process. In young females which have not yet begun gestation the diameter of the principal branches is twice that in the gravid females, but the ramifications are much less numerous, and each gland is limited to a small white tuft at each side of the uterus.

In females in an advanced stage of gestation these glands are seen to have taken on an excessive increase. On the dorsal surface there are four principal branches which arise from a common longitudinal trunk and pass over all the length of the growing larva. The lateral branches, passing round the sides and towards the ventral surface, divide up into innumerable ramifications, which, anastomosing with one another, produce a rich network of glandular tubes throughout the abdomen; the ultimate terminations end blindly. They penetrate into the interstices of the fat body, but there is no continuity between the two. The cellular walls are simply in intimate contact.

The epithelium of which these glands are composed presents different appearances in the different regions. In the proximal part of the organ, a little in advance of the union of the two principal trunks to form a common canal, the secretory cells are cubical, highly vacuolated on their internal aspect, and enclose a lumen which is circular on section and relatively large. Internally there is a fine layer of chitin, from which a series of spine-like projections pass into the lumen. The nuclei are small and spherical, the chromatin network indistinct, and there is a large centrally placed acidophile nucleus. In sections through the young ramifications, on the other hand, the secreting cells are higher, and the lumen correspondingly reduced. The cells are only a little vacuolized, the chromatin network is distinct, and the nucleus usually eccentric. There is no trace of the chitinous lamina internally.

Sections through the common duct show that it is in reality composed of two ducts which are united in a common muscular investment. The epithelium is replaced by a layer of small hypodermal cells, and the internal chitinous lamina is much increased, and presents an arrangement similar to that of the ducts of the spermathecae. The glands open on a small conical papilla which may be regarded as a sort of teat, since it is directed towards the mouth of the larva.

The cytoplasm of the cells of these glands has a remarkable affinity for stains, which makes the finer details of the histology difficult to follow. It is easily stained in the fresh state by neutral red, methylene blue, etc.

The fluid secreted by these glands is of a milk white colour when seen in bulk, and contains a large number of granules in suspension. Some of these are fatty, but the majority appear to be of an albuminous nature. The fluid is used, exactly as in mammals, for the nourishment of the young. It is not, however, entirely absorbed by the larva, but is retained in considerable quantity in the stomach, to serve for the nourishment of the larva after it has left the body of the parent.

Reproduction

The normal physiology of reproduction may be summarized as follows. The lowest follicles of the ovary produce eggs in turn, and as each is fertilized it passes down into the uterus. It has been shown by Roubaud that, if fertilization does not occur, the egg is retained in its position in the ovarian sheath, while the eggs which should be produced after it continue their growth up to a certain point. Fertilization, in fact, determines the passage of the egg to the uterus, but not the maturation of the eggs contained in the ovarian tubes. When it has passed into the uterus after fertilization the egg hatches, and a young larva emerges. The larva is free in the cavity of the uterus, but the walls of the latter, by virtue of their muscular tissue, contract around it, accommodating the size of the cavity to the size of the larva as it grows. The mouth of the larva is situated at the ' teat ' formed by the entry of the ducts of the milk glands into the uterus, and the larva, by a special apparatus, sucks the fluid from the glands into its stomach, which is always full under normal conditions. The posterior end of the larva is placed at the vulva, the muscles surrounding which are so arranged as to enable the cavity to be placed in communication with the external air, in order to allow the larva to breathe through the stigmata at its posterior end. The stay of the larva in the uterus is about ten to eleven days. When mature it is expelled by the contraction of the muscular coat of the uterus; its stomach at the time of birth is still full of the milk derived from the mother. It then crawls away to pupate.

The reproductive process in *Glossina* has been shown by Roubaud to be easily influenced by changes in the environment. As these have a direct bearing on the bionomics of the fly they will be discussed in that connection.

The Pupipara

Whereas the pupiparous habit in *Glossina* is markedly at variance with the method of reproduction in the rest of the Muscidae, in the Pupipara the habit is the rule, and forms the distinguishing character of the family. The subject is of great interest, and even before the practical importance of it was recognized it had already attracted a good deal of attention from entomologists. A very full account of the reproductive organs of *Melophagus* has been written by Pratt. The conditions in *Hippobosca* are very similar, and both resemble *Glossina* in the essential features, the similarity forming a good example of convergent development. The fact that *Glossina* is pupiparous does not, of course, indicate any direct connection by descent between that genus and the Pupipara; the latter form a class by themselves, and are only distantly related to the Muscidae.

Melophagus

In *Melophagus* (Plate XXX), the ovaries are arranged on the same plan as those of *Glossina*, but there are two ovarioles in each ovary instead of one. The same alternation in the production of the eggs is observed, but it is in this case a little more complicated, for not only do the ovaries alternate, but also the ovarioles in each ovary, so that only every fourth larva is produced from any given ovarian tube. The peritoneal coat of the ovary is much thicker than in most Diptera, and presents some remarkable peculiarities which have been described in detail by Pratt.

The *oviducts* present a striking feature, not found in any other Diptera, namely, the transformation of a part to form the receptaculum seminis. Each oviduct is short, and joins its fellow of the opposite side to form a slight dilatation in the middle line near the point at which the milk glands enter the cavity of the uterus, and it is here that the sperms are found in the fertilized female. In the virgin female the oviducts are not in line with the uterus as is usually the case, but join it at a right angle, that is to say, they are more or less perpendicular to the long axis of the body. When gestation is advanced the angle becomes very acute as the anterior end of the uterus passes forward with the growth in length of the larva.

The *uterus* is broad, and occupies a considerable proportion of the space within the abdomen, crowding the other viscera forwards when it becomes enlarged. It is compressed dorso-ventrally, and is held in position by large tracheae and muscles which run between it and the abdominal wall, as in *Glossina*. The wall is composed of a thick interlacing network of muscle fibres, internal to which there is the usual chitinous intima. In the lower part of the cavity the intima is thick, and is in continuity with, and of the same appearance as, the integument, of which the lower part of the uterus and the vagina are evident invaginations. In the upper part of the cavity the chitinous intima is very thin, and is thrown into numerous folds when the lumen is empty. The young larva is retained in this anterior portion for the first part of its period of growth, until its posterior end, which bears the stigmal plates, comes to lie in the vulva, through which its supply of air is drawn in.

There are two pairs of *milk glands*, both in *Hippobosca* and in *Melophagus;* one pair in the latter is rudimentary, and does not assist in providing nourishment for the larva. The functional glands resemble those of *Glossina* so closely both in their structure and disposition as to call for no further remark.

The Spermatozoa

The *Spermatozoa* of Diptera are long filiform bodies (Plate XXIX, fig. 6), which frequently exhibit active lashing movements. At one end there is a slight swelling containing the nucleus, which is difficult to stain properly. They do not present many differences in the different families, and their only importance from the present point of view lies in the possibility that they may be mistaken for parasitic organisms, such as spirochaetes or filaria. They are frequently seen free in dissections of male insects, having escaped through the rupture of the testes or the seminal vesicle, or in the female through rupture of the spermathecae. When once recognized, however, they are not likely to be mistaken for anything else.

The spermatozoa arise from the germinal cells of the testes by a process corresponding to that which produces ova in the female. Hereditary transmission of parasites through the male has not yet been suggested in insects.

THE NERVOUS SYSTEM

A brief note on the nervous system will suffice here, as all that is necessary for the parasitologist is to be able to recognize the parts when met with in sections and dissections.

Development

The nervous system of an insect consists of ganglia and nerves; the latter, as in the vertebrates, are either motor or sensory. The arrangement of the parts in the various groups is best understood by a reference to their origin. In a very simple insect there would be, theoretically, one ganglion, giving off motor nerves and receiving sensory nerves, on each side of each segment, and such a condition is in fact approached in some known forms. In later forms the ganglia have become fused with one another to a greater or less extent; the fusion results, as it has done in the vertebrates, in the gradual accumulation of the ganglia in the anterior part of the body, and particularly in the head. Each segment of the head may be supposed to have had originally its own pair of ganglia for the control of its own appendages. These, however, have become fused into a single more or less compact mass termed the brain. Similarly in the thorax, the three ganglia are usually, and always in the Diptera, fused to one mass. The abdominal ganglia may either remain distinct, or they may fuse with one another and even with the thoracic ganglion. In all cases the two bilateral ganglia of each segment are found to be fused with one another, the double ganglion lying in the middle line.

The brain, then, consists of six fused ganglia which belong to the head segments and supply the head appendages. As one might expect, the distinction between the several parts is not evident in the highly specialized Diptera, as far as the external appearance is concerned, and we find a rounded mass, generally considerably longer in the transverse diameter than in the antero-posterior, from which are given off nerves to the antennae, the palps, and other appendages. The lateral portions send out many radiating fibres for the supply of the compound eyes, and are distinguished as the optic lobes, while the middle portion, which may appear to consist of a single mass or two bilateral halves, is known as the central body. But of the six segments in the head three, or two where the third segment is wanting, as it is in the Diptera, are preoral, while the last three are postoral. The mouth lies, therefore, between the anterior and posterior parts of the brain, while the alimentary tract lies dorsal to the nerve cord and ganglia in the rest of the body. The tract has thus to pass through the brain to gain its subsequent position, and its anterior part is consequently encircled by a ring of nervous tissue. The particular part of the tract which pierces the brain differs in the different genera. In *Tabanus*, as already pointed out, the pharynx is anterior to the brain, which is pierced by the oesophagus, as is also the case in the Muscidae, whereas in the mosquitoes the pharynx is mainly behind the brain; the portion of the tract which pierces its substance is the chitinous tube connecting the buccal cavity with the pharynx.

The brain is thus divided into two parts, one which lies above the alimentary tract (strictly speaking, anterior to it), and is known as the *supra-oesophageal ganglion*, and one which lies below it, and is known as the *sub-oesophageal ganglion*. From the latter are given off two stout nerve trunks which soon unite with one another and pass backwards to the thorax, where they join the compound thoracic ganglion. From this emerge the nerves which supply the muscles of the thorax, and at its end a nerve trunk which passes to the first abdominal ganglion. Each of the abdominal ganglia gives off a pair of nerves for the supply of the muscles and organs of the abdomen, and sends a nerve cord to the ganglion immediately posterior to it.

The actual conditions to be met with in the Diptera are well exemplified by a comparison of *Anopheles, Tabanus* (Plate XXVII, fig. 1) and *Musca* (fig. 4, ibid.). In each of these the brain forms a compact mass which is pierced by the alimentary tract and gives off a large trunk on each side posteriorly. These nerve cords lie at first external to the oesophagus as it emerges from the brain, but as they converge to join one another they come to lie below it. In each of these forms the thoracic ganglia are fused with one another to form a large mass which lies in the middle ventral line in the anterior part of the thorax, but well marked differences are seen as regards the abdominal ganglia. In *Anopheles* these are six in number, and are well separated from one another. In *Tabanus* five abdominal ganglia can be distinguished, but they are set close together, looking like a string of small white beads. In *Musca* the abdominal ganglia are fused with the thoracic to form a large compound ganglion, from which many fine nerves pass backwards to the abdomen. There is thus a well-marked relation between the concentration of the nervous system and specialization in other directions.

The ganglion cells are of considerable size, and show up well in sections stained with haematoxylin, so that the separate parts of a compound ganglion can be readily recognized. In the brain there are certain curious and highly complex structures, known as the 'mushroom bodies', which stain brightly with eosin, and are conspicuous in sections of the head. These are connected with many commissures and tracts within the substance of the brain; for an account of them the reader is referred to Berlese's work.

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See also Gordon Hewitt, Minchin Patton and Cragg, Tulloch at end of Chapter IV.

NOTE.—For an account of embryology and development, which have not been dealt with in this chapter, see Berlese.

CHAPTER III

SECTION I

THE ORDER DIPTERA: ORTHORRAPHA—NEMATOCERA

THE Diptera form a well defined and highly specialized group of insects, easily distinguished, in the great majority of cases, by the presence of only one pair of wings; the second pair of other insects being represented by the halteres. The order is a large one, not less than 36,000 forms being known at the present time, while new genera and species are constantly being added. The study of the group has received a special impetus since the economic importance of many of the species has become recognized.

Metamorphosis and Early Stages

Before passing on to the classification and the detailed description of the important forms, it is necessary to refer briefly to the life history and early stages, and to explain certain connected terms in common use. Metamorphosis in the Diptera is always complete, the animal passing through the separate stages of egg, larva, pupa, and imago. The eggs vary greatly in size and appearance, and will be described under the species to which they belong. They are always minute, often invisible to the naked eye or nearly so, and are laid in or near the food of the larva, in numbers which correspond as a rule with the number of ovarioles in the ovaries. The larvae vary with their habitat and according to the family to which the imagines belong, the former factor exercising the predominant influence over their structure. Generally they are footless maggots, with an elongated and segmented body, consisting of a larger number of segments than can be distinguished in the adult. They may be aquatic or semi-aquatic in their habits, or they may live in decaying animal or vegetable matter, or in the excreta of animals. Although it is not necessarily the case that the larvae of allied forms resemble one another, as a general rule they do so, and a correspondence between the systematic position of the imagines and the structure of the larvae can be noted.

The more simple Diptera, such as are found in the Orthorrapha, have as a rule aquatic or semi-aquatic larvae, which move actively about by means of wriggling motions, or with the aid of posteriorly situated fins. The body is segmented, and the head, thorax, and abdomen may be well demarcated from one another. The larva feeds mainly on solid particles, such as animal or vegetable refuse, or on small animalculae, and is provided with mouth parts suitable for this purpose, the mandibles being often well developed. The alimentary tract is as a rule simple, and only slightly exceeds the length of the body, the coils being limited to the hind-gut. Larvae possessing a well defined head, with a pair of mandibles, are termed *eucephalous*. In the higher Diptera the larvae usually live in a rich food material, such as animal refuse, dung, etc., and neither need not possess biting mouth parts, the mouth being adapted for the ingestion of the rich liquid fluid in which their lives are passed. The same condition has led to a corresponding degradation of the rest of their structure. The head, for instance, since it has no longer to contain the mouth appendages and their muscles, is reduced until it cannot be recognized as such, when the larva is said to be *acephalous*; an intermediate form, in which the head, while yet recognizable, is inconspicuous, is termed *hemicephalous*. The larvae of the majority of Diptera are included under this latter group. Since larvae living in such material do not need to move about actively in search of food, they are generally unprovided with foot appendages, having at most small pseudopodia on the ventral parts of the segments, or thickened annular ridges at the junction of the segments, sufficient to enable them to gain a purchase on the substance in which they lie, while progression is brought about by rhythmical contractions and extensions of the body. On the other hand, as the outward form has become debased the internal structure has become specialized for the more rapid absorption and digestion of the food. The alimentary canal in these higher forms is always greatly increased in length, as it is in the adult, and is coiled up in the abdomen; the majority of the coils are situated in the posterior part, which is in consequence generally stouter than the anterior.

The respiratory system of the larva, owing to its constancy in certain groups, has been singled out as a point of importance in classification. Several forms are met with, dependent on the number and position of the stigmata. These are seldom placed segmentally, but are usually limited to the hind end of the body. From each stigma in this situation two lateral tracheae pass forwards through the body, giving off branches to the tissues as they go, and they communicate with the anterior respiratory openings when such are present. When there are stigmata on the first and last segments of the body (not counting the head) the larva is said to be ***amphipneustic***, while if they are limited to the posterior end the term ***metapneustic*** is employed. When stigmata are found along the sides of the body, an uncommon condition, the larva is said to be ***peripneustic.*** A larva may begin life in the metapneustic stage, and become amphipneustic later. The posterior stigmata are often conspicuous structures, and are usually recognizable with a hand lens. Since they differ in detail in closely allied flies, and often present the only recognizable distinctions between the larvae, they are of use in distinguishing species from one another, both in practical work when breeding for experimental purposes and for systematic classification.

In many of the aquatic larvae of the Nematocera the structure of the respiratory system is specially adapted to their mode of life. In the larger species of *Chironomus* the tracheal system is rudimentary and entirely closed, so that gaseous air is not taken into the body, the dissolved oxygen in the water, in all probability, being absorbed by the tracheal gills at the posterior ends of their bodies. These larvae, which live in tunnels at the bottom of pools, and even at great depths in lakes, have in addition a blood-red pigment—thus the name blood worm—which is believed to act as an oxygen carrier.

Another nematocerous larva which lives permanently below the surface of water, in this case well aerated water, is that of *Simulium.* It also has a closed respiratory system. The pupa of this type of aquatic larva has a large number of respiratory filaments, which are well adapted for the absorption of oxygen from water.

The larvae of the smaller Chironomidae, and of some of the Culicidae (*Corethra*), which live among weeds at, or near the surface of water, also have closed respiratory systems, but in this case the blood is colourless. Their pupae have respiratory trumpets, and are air breathers. The aquatic larvae of *Ceratopogon* and *Culicoides* are good examples of this type.

The larvae of Diptera usually cast their skins three times during the period of their growth, and although the moult is accomplished as a rule with little or no change except an increase in size, certain minor differences are to be noted in the several stages. This is of practical importance and must be taken into account in order to avoid mistaking the several moults of one species for different larvae. In mosquito larvae the difference lies mainly in the length and ramifications of the hairs of the exo-skeleton, the hairs tending to become more complex at a late stage in the life of the larva. In the Muscidae the form of the spiracles changes in a characteristic manner, the openings into the tracheae becoming much more convoluted.

The pupae of Diptera are of two main kinds. In one the larva casts its skin at the moment of pupation; in the other it pupates within the larval skin, which is then termed the *puparium*. In either case the pupae absorb no food, but remain passive while their tissues are reorganized to fit them for the final and reproductive stage of their life history. The larval skin is cast in the Orthorraphic flies. In them the pupa is often active, especially in the aquatic forms, but more usually it is motionless, and may be fixed to some object in its environment. Such a pupa is termed *obtecta*. In the higher Diptera the larval skin remains as an outer covering, within which pupation takes place, and the pupa is said to be *coarctate*. The distinction between the words pupa and puparium should be noted. The puparium has generally an elongate ovoid shape, with a rounded contour in cross section; the segmental markings can be faintly traced. The anterior and posterior stigmata can still be seen, and show the same markings as in the last larval stage.

The method of emergence of the imago from its pupa marks an important distinction between the two main groups of the Diptera. In the simpler forms it emerges through a T-shaped slit on the anterior part of the dorsum of the thorax, while in the higher forms the anterior end of the puparium is removed as a small circular cap, a method which has given to the group the name Cyclorrapha.

In some Diptera the life history is profoundly altered by the retention of the early stages within the body of the parent, where they undergo a part or the whole of their period of growth. When the larva is thus retained and nourished until it is mature, the fly is said to be *pupiparous*, a term which, though sanctioned by long usage, is a misnomer, for the larva must necessarily leave the body of the parent to pupate. The habit of producing larvae instead of eggs is found scattered somewhat indiscriminately throughout the Diptera, and occurs in varying degrees, as has already been pointed out in Chapter II. It is highly developed in the debased parasitic forms included in the Suborder Pupipara.

Because of the enormous size of the order and the additions which

Classification

are constantly being made to it, classification and identification are somewhat difficult and unsatisfactory. The field worker or parasitologist would do well, unless he has exceptional opportunities, to leave such matters in the hands of the specialist, and to content himself with a knowledge of those groups which are of practical importance. It is sufficient for most purposes to be able to ascertain with certainty, from a study of the external characters, which provide almost all the diagnostic features, that one is dealing with one species of fly and not two or more, and to be able to place the species in its proper genus. To do more than this requires in many cases an access to a voluminous and scattered literature, and also to the type specimens from which the species was originally described, or at least to a specimen named by a competent authority. The difficulty of identification has been greatly diminished by the keys which have been drawn up by specialists for such genera as contain species of practical importance. These will be found in this and the succeeding chapter, and it is hoped that with their assistance, and with some knowledge of external anatomy, the worker will be able to identify most of the important forms. A few named specimens are of great value for purposes of comparison. They may often be obtained in exchange for other material, or the worker may make a representative collection from his own district, and have the specimens identified.

The following arrangement of the groups is mainly taken from Williston, who has adopted the classification of Brauer.

The Diptera fall into three suborders, with secondary divisions, as follows :—

ORTHORRAPHA.	Larva with a jaw-capsule, or with a differentiated head. Pupa free or enclosed in the larval skin ; in either case escaping through a T-shaped slit on the dorsal side of the anterior end, or rarely through a transverse rent between the eighth and ninth abdominal rings. The imago has no frontal lunule or ptilinum.
Nematocera.	Antennae usually composed of more than six distinct segments, the two basal ones frequently differentiated from the rest; the flagellum always consisting of six to twenty or more segments, similar to one another. Palpi four or five jointed, and nearly always filiform. Wing venation simple or complicated. Larvae

	with either biting jaws or rudimentary mouth parts; in the latter case they have thirteen segments and are perineustic.
Brachycera.	Antennae very variable in structure, the two basal segments, as a rule, differentiated from the third, which varies much in shape and structure; it may be annulated or not; the arista is rarely dorsal, usually terminal. The venation is complex, more so than that in the Nematocera. Larva with a rudimentary mouth, and either metapneustic or perineustic.
CYCLORRAPHA.	Larva without a differentiated head. Pupa always enclosed in the larval skin—the puparium—the imago escaping through a circular orifice at the anterior end. Frontal lunule present, usually with a ptilinum.
Aschiza.	Antenna as a rule not composed of more than three segments, the third with a non-terminal arista. This group contains the three families Pipunculidae, Syrphidae and Platypezidae, in which the frontal suture is wanting.
Schizophora.	The antenna consists of three joints with an arista; frontal suture always present. The larva has no distinct head, and is always amphipneustic. This group is often divided into the Calypterae, in which the squamae are well developed, and the thorax has a well marked transverse suture; and the Acalypterae, in which the squamae are always small, and the thorax is without a complete transverse suture. These subdivisions correspond in the main to the Schizometopa and Holometopa of Brauer. The former is divided by some into the Anthomyiodia and the Muscoidea.
PUPIPARA.	Parasitic forms, often wingless or dropping their wings. Larvae born when ready to pupate. Very aberrant Diptera.

In this and the following chapter the families which contain important species will be particularly dealt with. For a more general account of the Diptera the reader should consult the *Cambridge*

Natural History (Insects, Part II), and for details of the genera Williston's *North American Diptera.*

THE NEMATOCERA

FAMILY CHIRONOMIDAE

Small midges from .5 to 14 mm. in length; proboscis somewhat long; antennae with four to fifteen segments, pilose in the female and plumose in the male. Eyes kidney-shaped; ocelli absent in all species. Thorax strongly arched, scutellum and metanotum small. Wings as a rule straighter in the male than in the female; costal vein terminating at the extremity of the third longitudinal vein; subcostal or auxiliary vein not well defined; first longitudinal vein distinct and abutting the anterior border of the wing; second longitudinal vein inconspicuous, and sometimes absent; third long vein well developed, often arising from the first and ending at the anterior border of the wing, rarely at the point. The fourth vein arises from the base of the wing, and is well developed up to the point at which it is united to the third vein; it may be forked. The fifth vein is nearly always forked; the sixth and seventh veins are incomplete or often wanting. The wing is rough or hairy, but never clothed with scales. The halteres are bare. The legs are never elongated, and the tibiae usually terminate in a short spur. The abdomen is long and slender.

The Chironomidae are common midges, many of which are nocturnal in their habits. During the rainy season in the tropics, they are seen in large numbers round a light, the majority of these prove to be males. Their larvae are the well-known blood-worms found in streams and stagnant pools. Some of them build for themselves characteristic tunnels of mud at the bottom of the pool, while others move about freely in the water or wet soil. A few pass their early stages under the barks of trees. The family is an enormous one, and is widely distributed. Kieffer recognizes five subfamilies, of which only one, the Ceratopogoninae, is known to contain blood-sucking forms.

The eggs of the Chironomidae are small and ovoid, or long and pointed at their extremities, and are laid either in a gelatinous string of mucus or separately. The larva usually consists of thirteen segments, and is eucephalic and amphipneustic; its head is directed downwards, and the mandibles are well developed. On the ventral surface of the first thoracic segment, and on the extremity of the last, there are one or two pseudopods armed with bristles or hooks. On the ventral surface of the eleventh segment, and the extremity of the twelvth, there are delicate finger-shaped processes, usually four in number; these are the tracheal gills. The pupa is free, and either lives floating in water without any movements, or rests on the bottom of the pool. It has a tuft of delicate white threads on the dorsum of the thorax, which serve as breathing tubes; or it may have a pair of respiratory trumpets.

SUBFAMILY CERATOPOGONINAE

Small to very small flies, from 1 to 2 mm. in length, seldom larger; antennae of fourteen segments, the first usually large and somewhat flattened, the last five in the male larger than the others; the whorls of hairs are relatively short in the female and long in the male. Palpi either of four or five joints, seldom of three. Thorax strongly convex, and not produced above the head. Wings flat and covering each other when in repose. Costal vein ending at the extremity of the third longitudinal vein; second longitudinal vein absent, and the first and third always larger and better marked than the others; third and fourth generally united by a transverse vein; the fourth, which is usually bifurcated, is not united to the fifth. Legs well developed and of medium length; femur often armed with spines on the lower surface. Larva without pseudopods or long hairs, or in some cases with thoracic pseudopods and with hairs.

The following genera contain blood-sucking species:—

GENUS TERSESTHES, TOWNSEND

Palpi three-jointed and longer than the proboscis; first segment the shortest, second segment swollen, the third straight and furnished with a tuft of hairs at its extremity; proboscis nearly as long as the head. Eyes kidney-shaped, and broadly separated at the vertex; ocelli absent. The antennae of the female are inserted into large circular depressions in the middle of the front, and consist of thirteen segments. The first segment is the largest, and is shaped like a flattened sphere; the second is more elongate but less broad, the third to the twelfth are subglobular and equal in length, and the thirteenth segment is an elongated cone. Thorax not produced above the head, but a little broader than it, and without a transverse suture. Scutellum prominent. Wing studded with minute hairs; first and second longitudinal veins better *developed than the others, and abutting the basal third of the wing border; third longitudinal vein reaching nearly to the point of the wing; fourth and fifth veins bifurcated: sixth and seventh not well developed. Legs slender, coxae not elongated, spurs on the hind tibiae prominent, those on the others weak; metatarsus elongated; pulvilli absent. Abdomen elongated, consisting of seven segments; ovipositor formed of two club-shaped processes.*

This genus at present contains the single species *T. torrens*, Townsend, which is found in North America, at a height of 7,000 feet; it bites horses and other animals, usually on the head, ears and eyes. Its life history is not known.

GENUS MYCTEROTYPUS, NOE

Noe created this genus for the two species *My. bezzii*, and *My. irritans* from the South of Europe, which are said to be voracious blood-suckers, biting human beings as well as animals, and causing inflammatory swellings. A. Weiss has recently described another species *My. laurae* from North Africa. According to Kieffer it is not quite certain whether the genus *Mycterotypus* is a good one; further observations on the species may show that they belong to one of the other genera of the Ceratopogoninae.

GENUS CERATOPOGON, MEIGEN

Head somewhat flattened in front, and prolonged into a moderately long proboscis. Antennae of fourteen segments in both sexes; first segment large and shaped like a flattened sphere, the succeeding eight or ten oval in shape, and in the male furnished with long plumose hairs; in the female the hairs, which may be long or short, are verticillate. The last segments are more elongate and have short hairs. Thorax strongly arched, but never produced above the head. Wings held in a horizontal position in repose, and usually rough owing to the presence of small hairs closely applied to the surface; third longitudinal vein either joined to the subcostal by a transverse vein, or united to it in part or the whole of its length. The fourth longitudinal vein is forked and joined to the third by a transverse vein. The fifth is also bifurcated, and there is often a forked vein, free at its basal end, between the third and fourth veins. The sixth and seventh veins are rudimentary. The legs are strong and of moderate length; the femora are neither spined nor swollen; the hind metatarsus is longer than or equal in length to the succeeding joint; the claws are simple and *equal; the empodium is well developed, and almost as long as the claws. The abdomen consists of eight segments; the male claspers have basal processes without any appendages; the terminal portion is long and gradually drawn out into a point.*

All the species of this genus are small, the limit of length being from 1 to 3 mm., and they are consequently not very easy to see when they bury themselves among the hairs of the host; they are easily recognized, however, when they become replete with blood. They often occur in large numbers, and are most frequently met with near water or thick undergrowth, seldom entering houses. They attack men and animals, and often cause great distress on account of their numbers and of the irritation produced by their bites. Some of the species show a preference for particular parts of the skin of the host, feeding only from the abdomen or legs; others select the face, and especially the margins of the ears and eyelids; only the females are blood-suckers.

Early Stages

The larva consists of twelve segments, including the head. Each segment is contracted at both ends, and partly or entirely covered with spines or small protuberances; eyes are absent. The antennae may be quite simple, consisting of a single unjointed spine-like segment, or of two or more joints. On the ventral surface of the first thoracic segment there is a leg-like appendage which consists of two pseudopods fused together; its surface may be smooth or covered with spines, and it is furnished at its apex with simple or bifid hooks. The anal segment is armed with two obliquely directed pseudopods, which are sometimes very short and fused together, and are always furnished with hooks. The larvae often have curious papillae on their dorsal surfaces, each of which may terminate in a single hair or a number of spines. These structures and the numerous long hairs are valuable taxonomic characters. In some forms, for example, *Forcipomyia*, the nymph has the remains of the larval skin attached to it, and in addition long hairs on its thorax and abdomen. The thoracic stigmata may or may not be prominent.

The larvae of some species are found under the barks of trees, on and under decaying leaves and wood, and in sap which exudes from trees; the majority, however, live in still or running water, especially where there is much algal growth, and where there are water plants, such as *Bromelia*. In Brazil Lutz has found the larvae of several species of *Ceratopogon* and *Forcipomyia* in crab holes, at the edges of mangrove swamps, and below the algal crust on the sand along the seashore.

Kieffer divides the genus *Ceratopogon* into the following subgenera :—

1.	Wings bare	**Atricopogon.**
	Wings hairy, at least in the female	2
2.	Hind metatarsus longer than the succeeding segment; or equal to it in the male, and longer in the female	**Ceratopogon.**
	Hind metatarsus shorter than the succeeding segment; or equal to it in the female, and shorter in the male	**Forcipomyia.**

There are some fifty or more species of *Ceratopogon* (sensu lato) from Europe, America, India, and Australia. Kieffer gives the following key to the six species of *Ceratopogon* (sensu restricto) at present recorded from India. It is not known whether they are blood-suckers or not.

INDIAN SPECIES OF CERATOPOGON

1.	Wings hairy	2
	Wings not pilose but with microscopical hairs	**indianus.**
2.	Wings with a white spot at the extremity of third long vein	3
	Wings with one or two black spots	4
3.	Anterior metatarsus a little shorter than the second segment, two to three times as long as broad	**albosignatus.**
	Anterior metatarsus much shorter than the second segment, a little longer than broad	**albonotatus.**
4.	Wing with a black spot on the radial cell (base of the wing); anterior metatarsus equal to two-thirds of the length of the second segment	**macrorhynchus.**
	Wing with two black spots on the anterior border; anterior metatarsus not half as long as the second segment	5
5.	Mesonotum dull, of chestnut brown, with long and scanty hairs; distal part of the fourth long vein without a stalk	**decipiens.**
	Mesonotum of a brownish black with a golden pubescence; distal part of the fourth long vein with a stalk	**auronitans.**

Ceratopogon (Atricopogon) indianus, Kief., from the Zoological Gardens, Calcutta; *C. albosignatus*, Kief., from Rangoon in February; *C. albonotatus*, Kief., from Calcutta; *C. macrorhynchus*, Kief., from Calcutta; *C. decipiens*, Kief., from Simla in May; *C. auronitans*, Kief., from Lower Burma.

Austen has recently pointed out that *Ceratopogon (Forcipomyia) castaneus*, Walk., is a common blood-sucker in Southern Nigeria.

Predaceous species of Ceratopogon

Major Lalor, I.M.S., has recently recorded from Burma a predaceous species of *Ceratopogon* which preys on *Anopheles fuliginosus, A.karwari* and *A.ludlowi*. About six per cent of *fuliginosus* caught in houses were thus attacked, the flies adhering to the abdomen and neck of the mosquito; some of the *Ceratopogon* contained blood, probably sucked up from the mid-gut of the mosquito. Dr. Stanton records another *Ceratopogon* which attacks *Anopheles fuliginosus, A.karwari*, and *A.sinensis* in the same way in

Kuala Lumpur, Federated Malay States. In this case the flies were invariably attached to the ventral surface of the abdomen, and always contained blood. It is doubtful whether the presence of blood in the *Ceratopogon* is more than accidental; probably its true food is the body fluid of the mosquito, as in the case with other predaceous flies (Asilidae). The connection between these species of *Ceratopogon* and mosquito-borne diseases, such as malaria, is a very remote one.

GENUS CULICOIDES, LATRIELLE

Minute midges usually measuring 1 mm., in length, sometimes 1.5 mm., nearly always of a dark brown or black colour, sometimes brownish yellow rarely whitish. The antennae consist of fourteen segments, the first eight or ten being globular or ovoid in shape, the remainder usually elongated, especially in the male. The wings are hairy, either over the whole surface, or only in parts; the third long vein is either united to the first by a transverse vein, or entirely blended with it; the fourth vein is either forked near the base, or towards the middle of the wing. The wings are often marked with dark spots and light clear circles in transverse rows of three, four, or more. The femora are not spined; the hind metatarsi are longer than the succeeding joints; the claws are simple and of equal length, and in some species have spines at their bases. The empodium is rudimentary, and is never more than half as long as the claws. When at rest these midges are very like those of the genus Ceratopogon.

About eighty species of this genus are recorded from various parts of the world. They have much the same habits and general appearance as *Ceratopogon*. The females bite man as well as animals, and both sexes are attracted to a light. One species *C. kiefferi*, Patton, which is common in Madras in the cold months, feeds only in the early morning, and is somewhat erratic in its habits; it occurs in large numbers on cattle on one day, and is practically absent the next. Sometimes many will be found on one calf, while others in the same herd are free from them. The males are often seen in large numbers on window panes, where they may be mistaken for 'eye flies' (*Siphonella*).

Culicoides kiefferi, Patton. Female (Plate XXXI, fig 1). Head, palpi and antennae light brown. Thorax light brown with a median dark band extending from the anterior end to about the centre, where it divides into two short branches. Abdomen light brown with faint

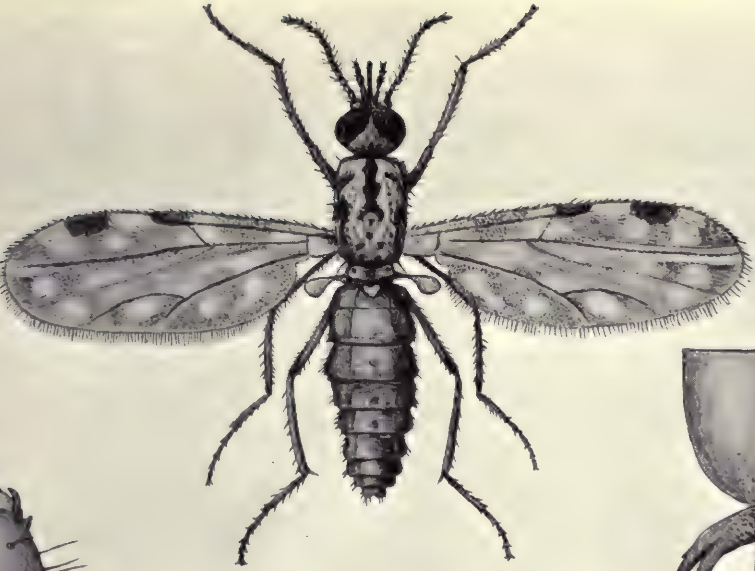

Fig.1.

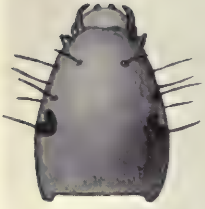

Fig.2.

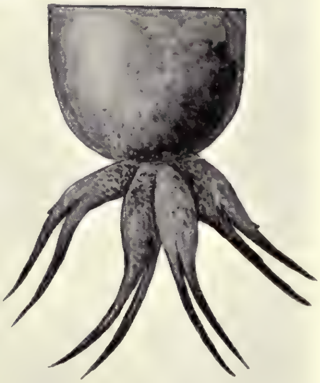

Fig.3.

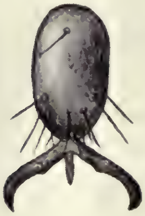

Fig.6.

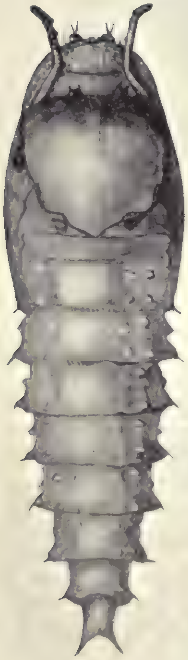

Fig.4.

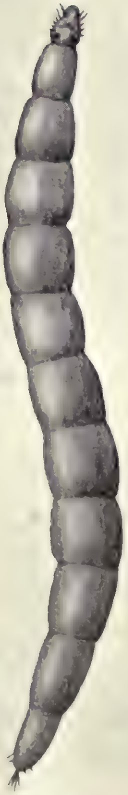

Fig.5.

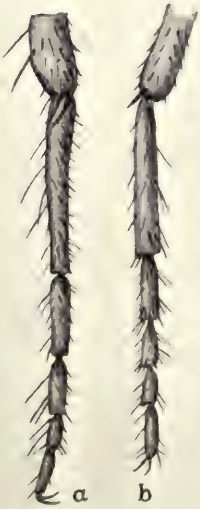

Fig.7.

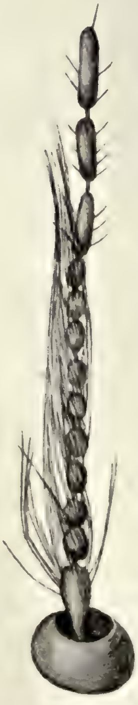

Fig.8.

PLATE XXXI

Figure 1. *Culicoides kiefferi*, ♀. × 30.
Figure 2. Head of larva of same enlarged.
Figure 3. Claws and empodium of hind leg of *C. kiefferi*.
Figure 4. Last segment of larva of same showing the tracheal gills extruded.
Figure 5. Larva of *C. kiefferi*. × 50.
Figure 6. Pupa of same. × 50.
Figure 7. (*a*) Hind leg: (*b*) Fore leg, of *C. kiefferi*.
Figure 8. Antenna of *C. kiefferi*, ♂.

bands and spots. Legs brown, fore metatarsus (Plate XXXI, fig. 7b), equal in length to the three succeeding joints; empodium (fig. 6) small and indistinct. Wing white, the surface clothed with fine hairs, and in parts with longer ones. There are two large dark brown spots, one about the centre of the costal border covering the entire third long vein; the other, which is also on the costa, is nearer the apex of the wing; there are in addition numerous lighter spots. The third long vein, which is closely adjacent to the first, is very pale and abuts on the costa about its centre; the fourth vein bifurcates about the centre of the wing, and the fifth divides opposite to the extremity of the third vein. Length 1.5 mm.

Early Stages

The *eggs* of *C. kiefferi* are small and ovoid in shape, and are deposited in a mass on green vegetable matter at the margin of running water. They hatch in three days and the larvae burrow into the green matter. If one places some of this in water in a white dish, and breaks it up with forceps, they come out and are then seen swimming about like giant spirochaetes; their rapid vibratile movements are extremely characteristic.

The *larva* (Plate XXXI, fig. 5), consists of twelve segments (including the head), all of which are smooth and almost entirely devoid of hairs. Unlike the larvae of all the other species of Chironomidae, that of *Culicoides* has no pseudopods on the ventral surface of the first thoracic segment. The head (fig. 2) is well developed, and the eyes are kidney-shaped. The dorsal surface and sides of the head are furnished with several small hairs, the two most prominent ones being situated on the mid-frontal region. The antenna of the larva of *C. kiefferi* consists of a single minute segment with a small hair at its apex. The mandibles are stout curved rods of chitin, and are armed with two teeth.

The first thoracic segment of the larva in some species has a single delicate hair on its ventral surface, and the anal segment is furnished with three or four simple hairs. The last segment (fig. 3) of *C. kiefferi* has four pairs of appendages which are deeply bidentate, and which can be extruded or withdrawn into the segment. These structures appear to correspond to the tracheal gills of other larvae. There are two long tracheal tubes which originate in the vicinity of the gills and give off numerous lateral branches as they pass forwards; there are no true stigmata.

The *pupa* (Plate XXXI, fig. 4), is very characteristic. Its surface is almost entirely devoid of bristles, but it has well developed spines at the sides of the abdominal segments, and knob-like processes on their dorsal surfaces. There is a pair of long breathing trumpets which arise from the sides of the mesothorax, their stalks are very narrow and are armed with several small blunt processes. The trumpets end somewhat like those of the pupae of the Culicinae. There are, in addition, several protuberances with hairs and spines at their extremities, and minute processes on the thorax. The pupa, which never has the larval skin attached to it, anchors itself by two prominent terminal spines; or it may float on the surface. The flies hatch out in three days.

Habitat of Early Stages: Breeding Technique

Lutz in a recent paper records having found the larvae of *Culicoides* in a variety of situations. The larvae of several species were taken from crab holes on the margin of a mangrove swamp, where they were living on the decaying food of the crabs. Other species were common in the salt water around the mangrove shrubs, as well as in the slimy matter at the edges of the swamps. In searching for the larvae in localities where the flies are common, green vegetable matter at the edges of streams should be collected and broken up in some water in a white tray; if there are any larvae in it they will be seen swimming about in the water. They should be transferred to a watch glass containing water and some of the green vegetable matter in which they were found by drawing them up with a pipette. In two or three days the pupae will be seen floating on the surface of the water at the edges of the watch glass. The larvae sometimes lie motionless at the bottom of the glass; these are not dead but are pupating, and will soon float up to the surface. The pupae should be transferred to a piece of moist filter paper and placed in a tube plugged with moist cotton wool. The flies, when they hatch, can be fed without difficulty on the shaved surface on the abdomen of a calf. Some specimens should be placed in two per cent solution of caustic potash for mounting, as this is the best way to study the structure of the legs.

GENUS JOHANNSENIELLA, WILLISTON

(Synonyms *Ceratolophus*, Kieffer; *Sphaeromyias*, Stephens.)

Allied to Ceratopogon and Culicoides. All the femora are without spines; the hind tarsal joints may be hairy or spinulose in both *sexes, or hairy in one and spinulose in the other; the claws are either equal or unequal in length, and are always simple in structure; the empodium is rudimentary.*

The habits of the mature insects of this genus are similar to those of the other blood-sucking Ceratopogoninae; their early stages are unknown, but will most probably be found in the same localities as those of the other genera.

One species *J. strictonota*, Kieffer, is described from Calcutta, but it is not known whether it is a blood-sucker or not. Neave records *J. fulvithorax*, Austen, from British East Africa; it is believed to be a blood-sucker.

Genus Haematomyidium, Goeldi

Antenna with fourteen segments, the last ones elongate; palpi with four segments, the second and third long. Wings with microscopical pilosity intermixed with long hairs; venation similar to that of Culicoides. Legs long, femora not thickened, and without spines; hind metatarsi about twice as long as the succeeding segment.

This genus was formed by Goeldi for a midge, commonly found in the houses of the natives of Para, South America, by whom it is called ' murium '. According to Goeldi the female is a blood-sucker. A single species *H. paraense*, Goeldi, is known, but according to Austen it is a true *Ceratopogon* (sensu restricto), and is probably identical with *C. phlebotomus*, Williston.

FAMILY SIMULIIDAE

Small thick-set, hunch-backed flies, usually of a dark colour, with short stout legs. The head is semicircular. Eyes round or kidney-shaped, holoptic and with moderately large facets on the upper surface in the male, dichoptic and with smaller facets in the female; ocelli wanting. Antennae short, cylindrical, and somewhat flattened, as long as or a little longer than the head, and consisting of ten joints. The two basal segments are distinct, but the remainder are more or less closely united. Palpi short, cylindrical, recumbent and incurved, consisting of four joints; the first short, the second and third equal in length, and the fourth longer and thinner; the palpi are as a rule longer in the female than the male. Proboscis short and stumpy, with well developed *labella. Thorax gently arched, and without a transverse suture; scutellum small. Abdomen cylindrical, broad, slightly ovoid and sometimes tabanid-like, consisting of eight segments, the first being the longest; external genitalia of male concealed. Legs well developed, never very long, femur broad and flat; tibia usually with a terminal spur; metatarsus much longer than the succeeding tarsal segments; the last joint is small; empodium rudimentary. The metatarsus is as a rule broadly swollen in the male. Wings large and broad, anterior veins thickened and spinulose, the remainder poorly developed and often almost invisible. The subcostal or auxiliary vein ends about the middle of the costa; the second long vein is wanting; the third arises from the first at its middle, and is forked; the fourth is a little curved, and is forked close to the base of the wing.*

This family contains the single genus *Simulium*, Latrielle. Altogether there are about one hundred species, distributed all over the world. Roubaud (1906) suggested splitting the genus into two subgenera as follows:—*Eu-Simulium*, in which the second hind tarsal joint is short in both sexes, is curved, and has a dorsal notch at the base. The pupa has a small number of respiratory filaments, an incomplete cocoon, and is solitary.—*Pro-Simulium*, in which the second hind tarsal segment is elongated, straight, and has no notch at the base. The pupa has a large number of respiratory filaments, a complete cocoon, and is found in company with others.

The Simuliidae are well known in most parts of the world on account of the great annoyance, and at times serious damage, which they may cause. In Europe and in India they are frequently called 'sand flies,' a name better reserved for the species of the genus *Phlebotomus*. In America they are known as 'buffalo gnats,' or 'turkey gnats,' the latter from the fact that they readily attack these birds and other fowls. Both in America and in the southern parts of Hungary these flies are often the cause of serious loss to farmers and stock breeders. They appear in swarms, attacking domestic animals of all kinds, and so irritate them by their bites that they manifest the most violent signs of fear and distress, shaking themselves, lashing their tails, and even careering wildly about in their efforts to rid themselves of their tormentors. Cattle will at times immerse themselves completely in water in search of relief. Birds are not exempt from their attacks, as their American name implies, and are often so tormented that they are driven from their nests. The flies bite them about the head and eyes, but will also crawl under the wings, and weakly birds often die from the irritation of the bites and from the loss of blood. Even human beings are not exempt, and in some parts of Brazil the species are so prevalent and troublesome at certain seasons, that the natives are compelled to keep fires burning in order to protect themselves. They are well known in the Amazon District as 'pium', and in South Brazil as 'barrachudo'. Fortunately they do not enter houses.

BRUNETTI'S KEY TO THE INDIAN SPECIES OF SIMULIUM

1.	Thorax black, at most with dull reddish brown tinge occasionally	2
	Thorax distinctly reddish brown, with short reddish hair	**rufithorax.**
2.	Thorax with grey shoulder spots and a wide greyish band on posterior margin	**grisescens.**
	Thorax ash grey with three narrow black stripes	**striatum.**
	Thorax without either grey shoulder spots or posterior bands	3
3.	Abdomen destitute of any sign of yellow hair	4
	Abdomen with short bright yellow hair, or with long rather shaggy brownish yellow hair	6
4.	Hind metatarsus much incrassated, nearly as long and large as the tibiae	**metatarsalis.**
	Hind metatarsus not so conspicuously incrassated, distinctly less in size than the tibiae	5
5.	Antennae wholly black. Length 2½mm.	**griseifrons.***
	Antennae reddish yellow at base. Length 1½mm.	**rufibasis.**
6.	Abdomen with normal short very bright yellow hair.	7
	Abdomen with distinctly longer, shaggy brownish yellow hair.	**senilis.**
7.	Abdomen with at least the first two segments yellowish, or brownish yellow; often several segments so coloured	**indicum.**
	Abdomen all black	**aureohirtum.**

JOHANNSEN'S KEY TO THE NORTH AMERICAN SPECIES OF SIMULIUM

1.	Ground colour of thorax and abdomen deep yellow	2
	Grey or black; its hairs may be pale	3
2.	'Femora with black tip, length of fly 2 mm.' Mexico	**ochraceum.**
	'Femora without black tips. Length 3 to 4·5 mm. Rocky Mountains	**fulvum.**
3.	Hind tarsi with its basal joint partly yellow; legs bicoloured	9
	Hind tarsi unicoloured	4
4.	Halteres dusky; thorax not striped	5
	Halteres white or yellow; the female with striped thorax and bifid tarsal claws	6

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* *Simulium griseifrons*, of which the female only is known, is probably S. *metatarsale*, of which the male alone is recorded; the broadly dilated metatarsus noted in the key is found in most of the males of the genus.

5. Body black; the female with dense yellow pile, her tarsal claws simple; the male with dense hair on the legs, his tarsal claws trifid. The wing with its radius three branched. Length 3 to 4. 5 mm. . . . . **hirtipes.**

'Body grey, legs reddish grey, feet black; length 3 mm'. This is said by Mr. Coquillett to be the same as *pecuarum*, Riley . . . . **invenustum.**

6. Males, eyes contiguous 7

Females, eyes separated by a distinct line 8

7. Thorax velvety black; legs reddish with black tarsi. Length 1. 5 to 2 mm. Compare here also *bracteatum* (male) 'with legs wholly brown' . . . . **meridionale.**

Thorax brownish black; legs usually pale; tip of tarsi not black. Length 2 to 4 mm. . . . . **pecuarum.**

8. Thorax with silvery white pubescence; legs brownish black, covered with whitish hairs. A small variety (less than 2 mm. long), from New Mexico has been named *occidentale*, Townsend . . . . **meridionale.**

Thorax with yellow hairs; legs reddish brown, covered with yellow hair; tip of tarsi blackish . . . . **pecuarum.**

9. Males, eyes contiguous 10

Females, eyes separated 20

10. 'Mesonotum wholly velvet black; grey spot on sides of the second, fifth, sixth and seventh segments of abdomen. Length 1.5 mm.' . . . . **bracteatum.**

Metanotum striped, or with greyish or metallic reflections 11

11. Dorsum of thorax with one or more longitudinal stripes 12

Dorsum unstriped 14

12. Thorax with four longitudinal stripes; posterior margin white; abdomen black. Sex not given. Cuban species . . . . **quadrivittatum.**

Thorax not so marked 13

13. Front and middle femora and tibiae wholly yellow; centre of mesonotum with a black vitta, elsewhere grey. Length 1·5 mm. Colorado species . . . . **griseum.**

Femora and tibiae wholly or partly brown 13*a*

13*a*. 'Femora and front tibiae yellow, their apices brown; middle tibiae brown, a yellow ring beyond the base, hind tibiae brown, the extreme base yellowish. Mesonotum marked with a narrow median and laterally with a very broad velvet black fascia.' Length 3 mm. New Mexico . . . . **virgatum.**

Front femora brown, tibiae brown on apical part . . . . 13*b*.

13 *b*. Mesonotum with two narrow grey stripes (sometimes quite indistinct) on a velvet black ground, in which there are scattered golden hairs . . . . **vittatum.**

'Mesonotum marked with a narrow median and slightly wider lateral black vittae.' Length 2·5 mm. Missouri . . **glaucum.**

14. Anterior femora yellow. Mexican species 15

Anterior femora black 17

15. Abdomen with the base of the second segment, and the sides of the third, fourth, and fifth yellowish white, tibiae fuscous black with yellow bases. Length 4 mm. . . . . . **mexicanum.**

Abdomen black 16

16. Metallic bluish black species; middle portion of fore tibiae, base of middle and hind tibiae, base of first and second joints of middle and hind tarsi, whitish. Length 2 mm. . **metallicum.**

Thorax fuscous and cinereous pollinose; the humeri pallid, fore coxae pale, middle and hind ones dark; femora pale at the base, black at the tip; tibiae black. Length 3 mm. . **cinereum.**

17. An oblique metallic streak extending inward from each humerus; posterior part of the thorax metallic. Length 2 to 2·5 mm. . . . . . **venustum.**

Humeral spots not metallic 18

18. Anterior coxae yellow; long hair on femora and hind tibiae; thorax velvet black with white pruinose margin (Greenland) **reptans.**

Anterior coxae black 19

19. Thorax velvet black, with oblique cinereous humeral spots, and usually two tiny metallic spots between them. Length 3 to 4 mm. . . . . . **pictipes.**

Thorax velvety black with two very narrow grey stripes and posterior margin; hind tibiae usually yellow at the base, hair on legs sparse . . . . . **vittatum.**

20. Thorax striped 21

Thorax without stripes 25

21. Dorsum of thorax with four longitudinal lines, posterior margin, white pollinose; abdomen opaque black. Cuban species . **quadrivittatum.**

Not with four stripes 22

22. Dorsum of the thorax with five stripes, the outer ones spot-like, the intermediate ones clubbed at the ends; abdomen with black fascia on each segment, produced posteriorly at the middle and the ends. Sometimes the last few segments have only three or five spots . . . . . **vittatum.**

Thorax with one or three stripes 32

23. With three stripes 24

'With an indication of a darker median vitta' (see 31) . . **griseum.**

24. Small species, length about 1·5 mm. 'Abdomen silvery, third and fourth segments wholly brownish, sometimes with a median spot on each; legs yellowish, tarsi blackish or brownish'. Species from Texas . . . . . **tamaulipense.**

Larger species 3 mm. or more in length 24*a*

24*a*. Middle tibiae brown with a yellow ring beyond the base; vittae of mesonotum brownish, the median vitta dilated posteriorly, wider than either of the lateral ones. New Mexico . . . . . **virgatum.**

Femora and tibiae greyish, sometimes quite pale, tips of tibiae black. Latero-dorsal thoracic stripes clubbed at the anterior end. Third, fourth, fifth, and part of sixth and seventh abdominal segments with velvet black fasciae; centre of 6, 7, and 8 greyish or dull brown . . . . . **pictipes.**

25. Abdomen without distinct black spots 26

Abdomen spotted 31

26. Abdomen black, covered with long yellow pile; legs yellow, the tips of the femora and tibiae, and all the tarsi except basal two-thirds of the hind metatarsi, brown . . . **bracteatum.**

Abdomen nearly bare 27

27. Body grey or cinereous 28
    Body brown or black 29

28. 'Body grey with a white milky lustre, especially the pleura and pectus. Legs tawny, femora and tibiae with irregular piceous bands, tarsi piceous. Length 2·5 mm. Hudson Bay Territory'. This is a synonym of *vittatum*, Zett., according to Mr. Coquillett (1898) . . . . . . **decorum.**
    Thorax fuscous or cinereous pollinose, humeri pallid, pleura pale cinereous, scutellum pale at the tip ; abdomen blackish ; fore coxae pale, middle and hind ones cinereous ; femora pale at the base, black at tip ; tibiae black. Length 3 mm. Mexican species . . . . **cinereum.**

29. Abdomen somewhat shining, yellowish grey or whitish at the sides, and yellow at the base ; legs brown, tibiae and fore coxae white, tip of tibiae and all tarsi black. European species, also occurring in Greenland . . . . . . **reptans.**
    Basal segments of abdomen opaque, distal fore segments somewhat shining black or brown. Two long hairs at the tip of the first and third fore tarsal joints 30

30. Legs reddish yellow, tarsi black, except proximal half of middle and hind metatarsi which are light yellow. Length 2 mm. (St. Vincent Island). This is a synonym of *pulchrum*, Phil., according to Hunter . . . . . . **tarsale.**
    Legs black, base of tibiae, first joint of middle and hind tarsi and sometimes base of femora yellow ; extensor surface of all the tibiae more or less whitish. A widely distributed and varied species . . . . **venustum.**

31. Length 1·5 mm. Front and middle femora and tibiae wholly yellow ; hind ones, except apices, also yellow. Colorado . **griseum.**
    Length 2·5 mm. Legs brownish black, distal part of femora, base of tibiae, and greater part of metatarsi light yellow. California . . . . **argus.**

LUTZ'S KEY TO THE BRAZILIAN SIMULIIDAE

1. Multicoloured species, the halteres and legs never entirely black 4
   Uniformly dark species, only the hair whitish, the wings colourless 2

2. The white hair thick but hardly visible to the naked eye 3
   The white hair thick and clearly visible . . . . . **flavopubescens.**

3. A little more than medium size, entirely black, from high altitudes . . . . **pernigrum.**
   A little less than medium size, more of a chocolate colour ; not an aggressive species . . . . **hirticosta.**

4. Ground colour of thorax grey to black 10
   Ground colour uniform 5

5. The sides of the thorax uniformly coloured 6
   The thorax black and gold, the marking varying . . . **varians.**

6. Colouring vivid 8
   Colouring dull 7

7.	Thorax reddish violet or reddish, often with dark stripes; claws not serrated; species of large size	**scutistriatum.**
	Thorax reddish brown; tomentum clear frosty; species of medium size	**pruinosum.**
8.	Thorax orange coloured	9
	Thorax red	**rubrithorax.**
9.	Edges of the thorax, and anterior sides of fore tibiae white	**perflavum.**
	Without any white; thorax with delicate tomentum	**hebeticolor.**
10.	Thorax without mother-of-pearl markings in the middle	12
	Thorax with mother-of-pearl markings in the middle	11
11.	Two anterior and submedian subtriangular spots	**incrustatum.**
	Mother-of-pearl-like longitudinal stripes	**minusculum.** **(amazonicum).**
12.	Tomentum golden to red; somewhat diffusely metallic or white	13
	Tomentum in small whitish tufts	**orbitale.**
13	The scale-like hairs of tomentum in groups or arranged in lines	14
	The hairs not arranged in any order	16
14.	The thorax without any clear edging	15
	The edging very clear; the legs very dark above	**subnigrum.**
15.	Scutellum dark	16
	Scutellum light brown often lighter	**subpallidum.**
16.	Large thick-set species with a dark silvery shimmer; from high altitudes	**distinctum.**
	Medium-sized species with a dull shimmer; from ravines, very aggressive	**pertinax.**
17.	Halteres externally reddish brown	13
	Halteres golden, with five clear golden stripes on the thorax; a medium-sized species	**auristriatum.**
18.	Halteres not very darkly coloured	19
	Halteres of a deep reddish brown; claws serrated; medium sized species	**infuscatum.**
19.	Claws not serrated; very small species	**exiguum.**
	Claws serrated; somewhat large species	**paraguayense.**

Simulium reptans, L. Johannsen gives the following translation of Schiner's description in *Fauna Austriaca*.

Male. ' Velvet black, dorsum of the thorax with a silvery white margin, ' spot-like on the humerus, broadly interrupted in front; visible only ' in certain lights. Pleura also with a whitish reflection; abdomen ' with silvery white spots on the second and on the last two segments, ' wanting in rubbed specimens; the posterior margin of the first segment ' with long and dense brownish cilia. Head black, face greyish white; ' antennae and palpi brownish black, the former more slender than is ' usual with the members of this genus, with whitish reflections on some ' parts. Legs dark brown; front coxae yellowish, fore tibiae silvery white ' outwardly; middle tibiae yellow at the base, hind tibiae likewise, though ' in less degree, light brown, with a whitish reflection; metatarsi of the 'hind legs yellowish at the base; the hairs of the fore and hind femora, 'and particularly on the extensor surface of the hind tibiae, conspicuous. 'Halteres bright yellow; wings purely hyaline, with delicate and transparent veins, those of the anterior margin being somewhat thicker and 'more conspicuous; the wing surface with a golden brown reflection; 'the media not petiolate. The short, scattered hair of the thorax seldom 'distinct, the colour of the legs variable in intensity.'

Female. 'In colouring does not resemble the male in the least. The 'ground colour is blackish brown; the dorsum of the thorax covered with 'a depressed yellow pile, on the margin with a whitish reflection, on the 'centre with a greyish reflection, the pleura greyish white. Abdomen 'somewhat shining; on the sides whitish or yellowish grey; on the venter, 'at least at the base, in living specimens, yellow, which is continued 'around on the dorsum in some specimens, usually not distinct in dried 'specimens. Legs brown, usually paler than those of the male; the 'tibiae, with the exception of the tip, and the fore coxae whitish or 'yellowish white, the tips of the tibiae and tarsi black, the basal half 'of the hind metatarsi and sometimes also the extreme base of the 'following joint yellowish. Front and face grey; antennae and palpi 'brown, the former paler at the base. In other particulars as with 'the male. Length 2 to 3 mm.'

Simulium reptans is widely distributed throughout Europe, and is stated by Sambon to be the invertebrate host of the parasite (?) of Pellagra. In this connection it is interesting to note that it is not found in the United States, in some parts of which pellagra is very prevalent.

Simulium indicum, Becker. A large black species (2½ mm.), with a dark thorax and abdomen, except the last segments of the latter, which may be yellow or yellowish brown. Femora and tibiae yellow on their basal halves and black at their apices. It is widely distributed in North India, where it is known as the 'Potu Fly'; it is recorded from Baltistan at an altitude of 10,000 feet.

Simulium striatum, Brunetti (Plate XXXII, fig. 1). Thorax grey with a few golden hairs, and with three moderately narrow dark stripes commencing just behind the anterior margin, and fading away before the posterior margin is reached; sides of thorax dull grey. Abdomen black. Fore tibiae dark brown, posterior tibiae yellowish on basal half; hind metatarsi pale yellow with a black tip. This species was originally described from Ceylon. It is very common in Kodaikanal (6,000 ft.) South India, where it breeds in all the hill streams. Its egg, larva, and pupa are depicted on Plate XXXII.

PLATE XXXII

Figure 1. *Simulium striatum*, ♀. ×16.
Figure 2. Egg mass of same on a blade of grass.
Figure 3. Pupa of same. ×14.
Figure 4. Larva of same. ×14.
Figure 5. Single egg of same, highly magnified.
Figure 6. Ventral view of head of larva of same, showing the mouth parts.
Figure 7. Dorsal view of same, showing antennae.

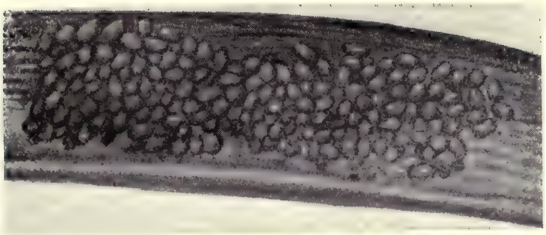

Fig. 2.

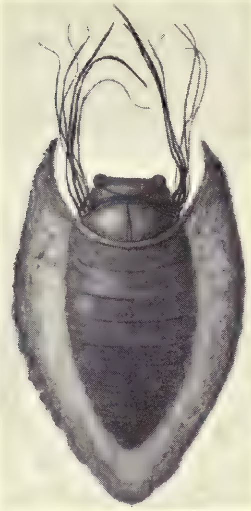

Fig. 3.

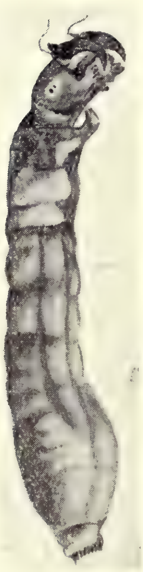

Fig. 4.

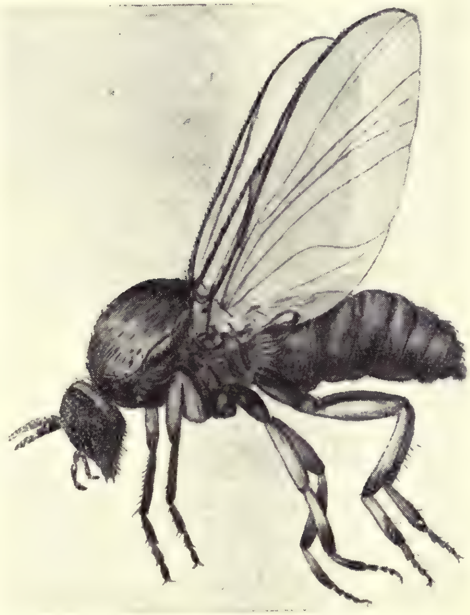

Fig. 1.

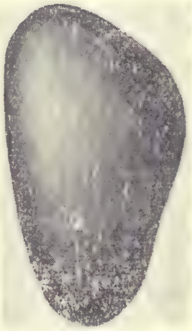

Fig. 5.

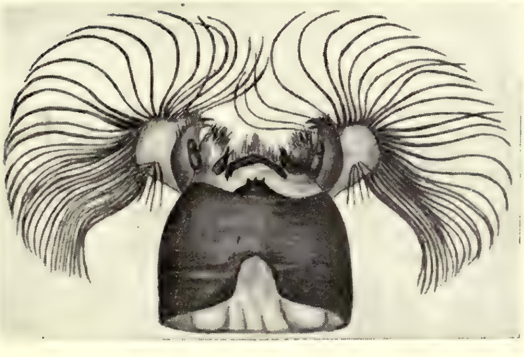

Fig 6.

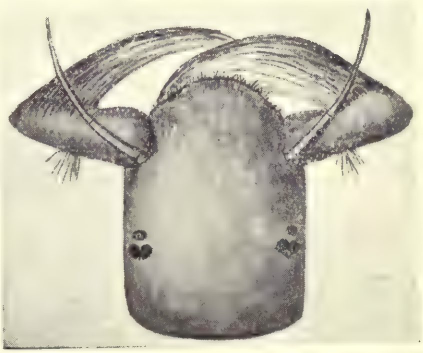

Fig. 7.

Simulium damnosum, Theobald. Body of a uniform black colour, antennae and palpi black. Thorax dark with golden hairs; abdomen black with short dark hairs. The metatarsi and first two tarsi of the fore legs are swollen. Larva large and of a dark colour, with a pigmented patch at the sides of the first thoracic segment. Pupa with a bifid comb of tubes which do not project much above the cocoon. *S. damnosum* is the well-known 'Jinga Fly' of Uganda, and is widely distributed throughout Equatorial Africa.

Bionomics of Simulium

At certain seasons Simuliidae appear in swarms and attack animals and even man. They are generally met with in the vicinity of streams, especially where there are woods. They usually bite larger animals on the abdomen, either near the scrotum or udders, or on the fore legs. Other favourite places are the inside and along the margin of the ears, and round the eyes. They are most active during the early part of the day, from sunrise till about 10 a.m., when they retire to rest on the under surfaces of leaves close to the ground. They begin biting again towards evening, and may continue to do so till late at night, especially during moonlight nights. When attacking man they often settle on the forehead, back of the neck and the ears, and cause considerable annoyance by trying to crawl into the eyes and nose; they may also bite the ankles, even through stockings. The bite is sharp and stinging and causes considerable irritation.

Early Stages. Plate XXXII

In 1795 Schönbauer described the early stages of the 'Columbacz gnat', *Simulium columbaczence*, Schön., and drew attention to the remarkable fact that its eggs are laid on leaves, blades of grass, etc., *under* water, and that the larvae attach themselves to any fixed object floating in the water; when about to pupate they spin a cocoon on the support. The eggs (figs. 2 and 5) are small ovoid objects, somewhat yellowish in colour, usually more pointed at one end than at the other; they are often distorted, and then project at one side. They are enveloped in a gelatinous substance, and are spread out in an uneven layer either on blades of grass or dead leaves, or on stones, etc., below the surface of the water, usually where it is running swiftly; they never lay their eggs in stagnant pools. Some species oviposit only on stones, others on any support under the water, especially in places where it rushes rapidly round a bend. When about to lay her eggs the female crawls down to the edge of the water, inserts a part of her abdomen beneath the surface, and deposits the eggs with their accompanying gelatinous substance. They hatch in about three or four days, according to the temperature. The larvae at once attach themselves to the support by their posterior suckers, and can be seen waving about in the water.

Structure of the larva and pupa

The body of the larva is cylindrical, gradually broadening out posteriorly in the shape of an Indian club; in some species the increase in breadth is very gradual, while in others it is somewhat abrupt, and thus gives the body a constricted appearance in the middle third. The colour varies somewhat, dark olive green being the predominant shade, and the one which harmonizes best with the leaf or other support to which the larva is fixed. The body is composed of twelve rather indistinct segments, five of which usually form the dilated posterior end. On the ventral surface of the first thoracic segment there is a well developed forwardly-directed pseudopod, which represents two legs fused together; it is conical in shape, and is armed at its apex with a circular row of short hooklets or spines. When the larva is touched the anterior pseudopod retracts.

On the last segment there is another pair of pseudopods joined together to form a flattened, sub-cylindrical sucker, armed with a row or rows of hooklets arranged in regular transverse series. True stigmata are wanting; the tracheal tubes end on the ventral side of the suckers, where they join three short, cylindrical tentacles, the *anal gills*; these finger-like processes, which may be simple or branched, can be retracted, but when it dies in still water, or when the larva is dropped into spirit, they are always extruded. The head is large, somewhat flattened, and almost rectangular in shape, with two black approximated lateral eye spots, the anterior of which is usually the smaller of the two; the posterior is reniform in shape. The labium is broadly rounded off in front; the antennae are long and attenuated, and consist of three joints. The first is very small and inconspicuous; the middle, which is longer, is about half the length of the last. Situated directly behind the antennae there are two broad, somewhat flat arm-like processes, the feeding brushes, each furnished with a long fan-like fringe of dark hairs; if the larva is examined with a lens when under the water, they can be seen to open and close in rapid succession, the long hairs whirling round and drawing in small objects towards the oral opening. When the larva is dropped into spirit, they spread out and can then be easily studied.

The mandibles are stout blades of chitin, armed with short stiff spines at their inner ends as well as long delicate hairs; the maxillae are somewhat triangular plates of chitin, densely covered with hairs arranged in a tuft, and usually with one slender spine just below their apices. The palpi are short, consisting of three joints. The labial plate may be broad or narrow, and is armed at its anterior end with three to five or more teeth, the external ones usually bidentate; these teeth are useful in identifying the species. The alimentary tract of the larva is a simple tube, at either side of which there are two long glands, which secrete the gelatinous substance from which the anchoring threads and the silken fibres of the cocoon are made. When the larva is about to pupate, it spins the characteristic case by first fastening a thread on one side of its support, and then carrying the other end over to the opposite side; repeats the process until it has constructed a heart-shaped pouch, deeply scooped out at its anterior end, and pointed posteriorly; this is attached by its sides to the support, which may be the back of a leaf or twig, or the surface of a stone.

Miss Phillips has made some detailed observations on the spinning of the cocoon of *Simulium pictipes*, Hagen, which she describes as follows:—'In spinning, the thread issues from the mouth and is placed 'in the different positions by the thoracic proleg. The head is bent 'down, and with the proleg the thread is drawn around the body and 'other threads placed or twisted in all directions, until a very irregular 'network is formed, covering the whole of the body, except the head. 'The skin of the head is then cast off, and the insect pulls itself out 'of the skin of the body, leaving it whole. The cast skin may often 'be found in the cocoon, with the pupa. The cocoons are commenced 'at the upper margin and spun continuously down to the caudal end, 'where several threads are drawn from the cocoon and attached to the 'last one or two of the body segments of the pupa. The threads hold 'the pupa very firmly, and are always found when the pupa is pulled 'out of its case.'

The larvae feed on small crustaceans, such as Copepods and Isopods, small polyps, fresh water sponges and small animalculae, which are present in all streams. Their movements are interesting to watch when crowded together on a leaf. When a larva sways too much to one or other side, and touches its fellow, both rapidly retract. They can crawl up their supports with great agility, the loops being rapidly made. Before it moves the larva always fixes its thread to the support so that if it becomes detached it can crawl back in safety.

The *pupa* (Plate XXXII, fig. 3) is ovoid in shape the anterior end forming a broad transverse ridge, at the end of which the raised antennal sheaths can be distinguished. The thorax is gently convex, and has attached to its lateral edges a tuft of from six to eight or more long filamentous hairs, or thick bifid processes, the *thoracic gills*. Each filament projects freely from the open end of the pouch. The structure and number of the gills are useful taxonomic characters. The abdomen may or may not be furnished with spines, and usually has at the tip two bent or recurved hooks, by which it is anchored to the bottom of the pouch. At first the pupa is of a light mahogany colour, but it becomes slowly darker, until just before the imago emerges it is almost black.

Bubbles of gas now begin to collect under the pupal skin, and, when it splits horizontally along the middle line, the fly rises to the surface in a bubble. It crawls on the water or is washed down for a short distance, but soon clings to some support, and then flies away and settles on some neighbouring twig or blade of grass.

Breeding Technique

The essential factors governing the well-being of the larvae of *Simulium* are water in rapid motion, and a support on which to fix themselves. These conditions are always available in streams coming from some elevated place. A sudden bend, a declivity, or any obstruction will cause an acceleration in the motion of the water. In such places blades of grass, dead leaves, sticks, and stones accumulate, and it is here that the larvae are found in large numbers. It is quite futile to attempt to breed out the flies by keeping the larvae and pupae in any kind of aquarium, for they are sure to die. Newstead states that he has bred out the imagines by placing the leaves, stones, etc., to which the pupae were attached in a glass jar covered with fine muslin netting, merely keeping them moist; in some cases the insects hatched out of pupae which were quite dry.

In attempting to breed *Simulium*, it is best to place some simple apparatus around the larvae in the water, and not to remove them to trays or dishes. A tin frame, similar to the top of the fly jars (see Chapter 4 and Plate XLIV, fig. 5), should be fixed over the place where the larvae are attached, either by burying it in the sand, or tying it with string to some supports at the sides. When the larvae have pupated, a fine meshed net can be fitted over the frame, and in this way the water will still flow past the pupae, and the flies, which will hatch out under natural conditions, will settle on the net after rising to the surface. As the males are not blood-suckers they can seldom be obtained except by breeding them out.

Lutz suggests another simple way of breeding *Simulium*. A large lamp chimney is partially immersed in the water, horizontally and in the direction of the current, and the leaf or twig to which the larvae are attached is then passed into the chimney; the water flows through the chimney, so that the larvae remain under natural conditions; when they pupate the ends of the chimney should be covered with fine netting, which will prevent the flies from escaping.

FAMILY PSYCHODIDAE

Small to minute moth-like gnats with narrow depressed heads; frons wide in both sexes; ocelli wanting. Antennae long, as long as the thorax and head together, with a beaded appearance, and thickly covered with hairs; each antenna is usually composed of sixteen segments, the two basal ones being short and cylindrical. Palpi recurved, covered with hairs and scales, and consisting of from four to five segments. Proboscis very short, or as long as the head. Thorax raised, arched, and covered with dense hairs; scutellum rounded. Abdomen cylindrical, composed of from eight to ten segments; male genitalia prominent, consisting of two or three pairs of appendages; in the female the ovipositor may be prominent or concealed within the last segment. Legs stumpy, or very long and slender, covered with hairs and scales; claws small. Wings large, oval or lanceolate in shape, covered with hairs or scales, when at rest either held in an arched manner over the abdomen, or in an upright position; the margin is fringed with hairs. The costal vein is continuous round the wing; the other veins are well marked, and are almost all longitudinal and hidden by hairs or scales. Subcostal vein very short. The second long vein arises near the origin of the first, and may be forked either once or twice; the front vein, which is often spoken of as the second division of the second vein, is considered by some to be a branch of the third vein. In any case there appear to be either one or two simple longitudinal veins between the second and fourth. The vein (3rd) just anterior to the posterior forked vein (4th) nearly always terminates at or near the tip of the wing. The fifth and sixth longitudinal veins end at the border of the wing, and the seventh, if present, is always short. The cross-veins are very indistinct, and are situated in the basal half of the wing. The supernumerary and the mid-cross veins, situated at the base of the third long vein are the most prominent. The eggs of the Psychodidae are laid in damp earth, where there is green algal matter. The larvae are cylindrical, the last segment often ending in a short stiff stigmatic tube. The pupa *resembles that of the* Culicinae *is inactive, and often has respiratory trumpets.*

The Psychodidae are small hairy moth-like flies, commonly known as 'owl midges'. They are frequently seen in dark corners, on windows, or in damp decaying grass, and about horse and cowdung; their flight is feeble, and is accompanied by a peculiar buzz. Nearly all the species are hairy, and hold their wings arched over the abdomen, except the Phlebotominae, in which the wings are raised above the body. As far as is known at present, only the genus *Phlebotomus* contains blood-sucking species, the well-known 'Papataci' or 'Sand Flies'. These insects have attracted considerable attention during the last few years on account of the connection of *Phlebotomus papatasi*, Scopoli, with Papatasi or Phlebotomus Fever.

This febrile condition was described many years ago by Pym, an army surgeon in Malta, but it remained one of the obscure fevers of unknown origin until 1908 when Doerr studied it in Herzegovina. This observer proved that the infection was transmitted by *P. papatasi*, and Birt and others have since confirmed his work. It is now known as the result of actual transmission experiments in Malta, Crete and in London, that the fly is infective seven to ten days after ingesting the virus of the disease, which is present in the blood of a sick person during at least the first day of the fever. The disease is probably widely distributed, and is believed to occur along the North-West Frontier of India and in parts of South America.

The family Psychodidae is usually divided into two subfamilies, the Psychodinae and the Phlebotominae, which may be distinguished by the following characters:—

Subfamily Psychodinae. Owl-like midges densely covered with hairs. Seventh longitudinal vein without exception well developed. Second vein forked once, or, as some consider, twice; the first division is then very near the base of the wing, the lower branch running out to the tip; the upper branch again forks nearer the base than the middle of the wing. Proboscis short, not armed for piercing; ovipositor strongly chitinized and ending in a pair of flap-like valves; male genitalia consisting of two or three appendages.

Subfamily Phlebotominae. Not such hairy moth-like flies. Seventh longitudinal vein entirely absent, or if present markedly reduced; in a few instances it runs to the wing border. The second longitudinal vein forks about the middle of the wing, and the upper branch again divides nearer the tip than the middle of the wing. The proboscis in the genus *Phlebotomus* is longer, and is armed for piercing; the ovipositor is hidden; the male genitalia consist of three pairs of appendages.

WILLISTON'S KEY TO THE COMMON GENERA

1.	Two simple longitudinal veins between the forked veins	**2**
	One simple longitudinal vein between the forked veins	**4**
2.	The first simple vein arises from the forked vein much beyond the anterior cross-vein	**Phlebotomus.** **(Phlebotominae).**
	The first simple vein arises near the anterior cross-vein	**8**
3.	The second simple vein ends at, or near the tip of the wing	**Psychoda.** **(Psychodinae).**
	The second simple vein ends distinctly beyond the tip of the wing	**Pericoma.** **(Psychodinae).**
4.	The seventh longitudinal vein (the most posterior one) is not much shorter than the sixth	**Trichomyia.** **(Phlebotominae).**
	The seventh longitudinal vein is very short	**Sycorax.** **(Phlebotominae).**

Phlebotomus is often confused with *Psychoda* and its allies, but the following points will help to distinguish them :—

Psychoda: small stumpy flies with short legs and bushy wings, *Phlebotomus:* more elongated and have longer legs and narrower wings, which are nearly always held away from the body. Should there still be any doubt, drop a specimen of the fly into two per cent caustic potash solution, clear it and mount it entire, or dissect off the head and mount it alone. In *Phlebotomus* the mandibles and maxillae are serrated and obviously formed for piercing; in *Psychoda* they are poorly developed and not formed for piercing.

GENUS PHLEBOTOMUS, RONDANI

Small psychodids with relatively large hairy wings which are held upright, and are devoid of scales. Palpi of five joints, cylindrical in shape; according to Newstead *the third palpal segment of some species is provided with minute spines, probably of a sensory nature. The spines may be squamiform and with short pedicels* (*P. minutus*) *or sapthuliform and with long curved pedicels* (*P. papatasi*). *Antennae long and slender, consisting of sixteen segments, the first short and thick, the second rounded, the third the longest, and the remainder swollen at their proximal ends; in some species several of the segments have geniculated spines* (Newstead). *Proboscis longer than the head, and conical in shape*

Thorax covered with hairs. Abdomen with eight segments, narrow and thickly furnished with hairs. Male genitalia (Plate XVII, fig. 4) *consisting of three appendages* (see page 86). *Female organs indistinct, forming superior and inferior leaf-like appendages, which are covered with hairs ; a true ovipositor is wanting. The second longitudinal vein is forked twice, once about the middle of the wing, and a second time at the outer third ; the first branch is spoken of in the above key to the genera as a simple longitudinal vein, which, with the third, lies between the forked veins.*

Newstead gives the following key to the Maltese species :—

A. Abdominal hairs recumbent.
  (*a*) Integument black. Large species. Palpi with second segment longer than the third . . . . . . **nigerrimus.**
  (*b*) Integument ochreous. Small species. Palpi with second segment one-half the length of the third . . . . **minutus.**
B. Abdominal hairs more or less erect.
  (*a*) Legs in both sexes relatively short, average length of hind leg, 3 mm. Terminal segment of superior clasper of male scarcely half as long as the inferior clasper . . **perniciosus.**
  (*b*) Legs in both sexes relatively long ; average length of hind leg, 4 mm. ; terminal segment of superior clasper of males slightly longer than the inferior clasper . . . . **papatasi.**

Phlebotomus nigerrimus, Newstead. A black or brownish black species closely allied to *P. papatasi*, but with the hind margin of the wing strongly arched, and the sixth longitudinal vein short, ending about the centre of the hind margin of the wing. It is a rare species and only occurs in certain parts of Malta (Gozo) ; the male is unknown.

Phlebotomus minutus, Rondani. A dull golden ochreous species of small size (1.5 to 2 mm.). The second palpal segment is about one-half the length of the third ; fourth segment shorter than the third ; fifth segment long and slender. The third antennal segment is relatively short ; the hairs on the abdomen are recumbent. It is very active in captivity, leaping about, and whirling round, and according to Newstead it can be distinguished from all the other Maltese species by this habit alone. Marett states that it breeds in the rubble walls, bastions, and ground ventilators in Malta.

Phlebotomus perniciosus, Newstead. A somewhat dark species with or without a reddish brown spot on the thorax ; it is smaller than *papatasi* with which it may be confused. Its legs are also shorter, and the male genitalia are smaller. The female is darker than that of *papatasi*. It is widely distributed in Malta, and is very common during July, August, and

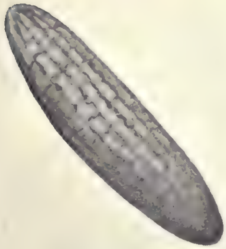

Fig. 1.

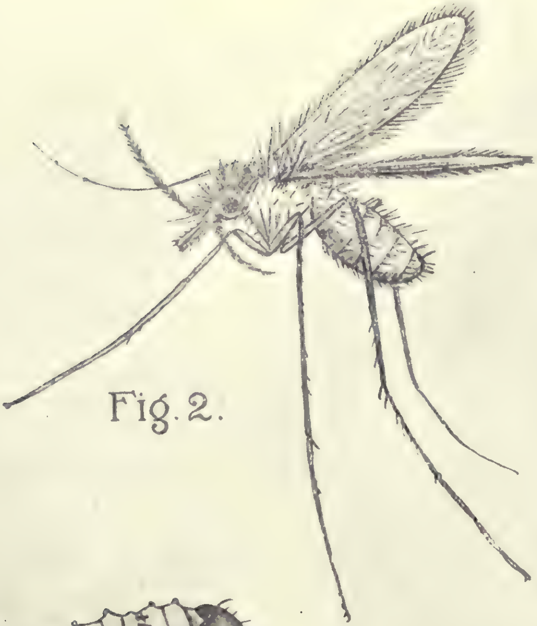

Fig. 2.

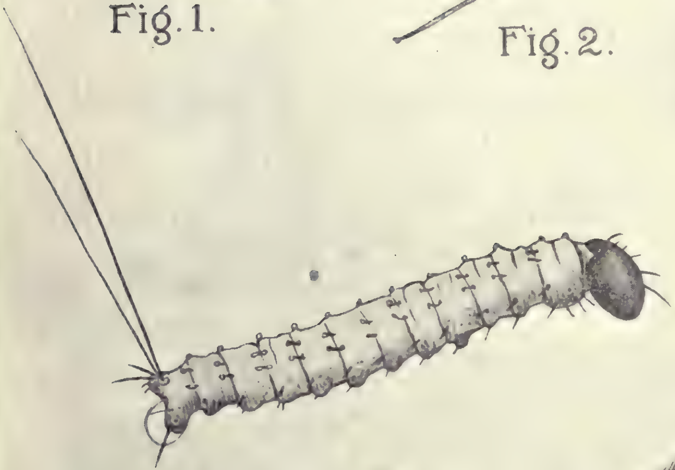

Fig. 3.

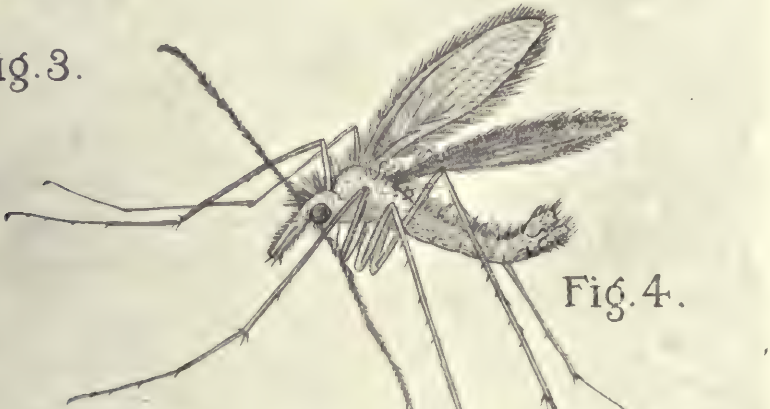

Fig. 4.

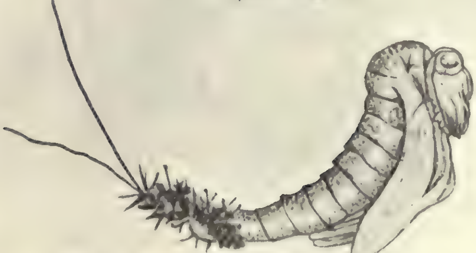

Fig. 5.

PLATE XXXIII

Figure 1. Egg of *Phlebotomus papatasi*, much enlarged, to show the reticulated surface.
Figure 2. *Phlebotomus papatasi*, ♂, enlarged about 20 times.
Figure 3. First instar of larva of same enlarged.
Figure 4. *Phlebotomus papatasi*, ♀, enlarged about 20 times.
Figure 5. Pupa of same showing larval skin attached, enlarged.
All the above after Newstead.

the early part of September. According to Marett it has the same breeding habits as *minutus.*

Phlebotomus papatasi, Scopoli (Plate XXXIII, figs. 2 and 4). A pale yellowish grey species, sometimes with a dark coloured fringe to the costa and the hind margin of the wing. The external genitalia of the male are much larger than those of any of the other Maltese species, as can be readily seen with the aid of a hand lens. The wing is narrower, but the posterior margin is more distinctly arched than the anterior. It is larger than its near ally *perniciosus,* paler in colour, and has longer legs. This species is known to transmit the parasite (?) of Phlebotomus Fever. It is widely distributed in Southern Europe, North Africa, and the whole of North India. According to Marett in Malta, it breeds in caves and embankments.

Annandale and Brunetti's Key to the Indian and Cingalese species

1. The second longitudinal vein forks nearer the middle of the wing than at one-fourth. Petiole of first submarginal cell always much longer than one-third of the cell's length, except in *himalayensis,* in which it forks exactly at one-third 2

The second longitudinal vein forks exactly at one-third of the wing. Petiole of first submarginal cell only one-third as long as the cell 8

2. Tip of first longitudinal vein, either about half-way between fork of second vein and tip of wing, or nearer tip of wing. . . . 3

Tip of first longitudinal vein distinctly nearer fork of second vein than tip of wing 5

3. Fork of upper branch of second longitudinal vein nearer fork of second vein than tip of first vein. Wing comparatively lanceolate; fork of second vein beyond that of fourth vein. Colour of insect yellowish grey. Genitalia of male with three chaetae at tip . . . . **himalayensis.**

Fork of upper branch of second longitudinal vein nearer tip of first longitudinal vein than fork of second vein 4

4. Wing broader; fork of second vein before that of fourth vein. Colour of insect dark greyish brown. Genitalia of male with both the middle chaetae median. Hind femur between one-half and three-quarters as long as its tibiae, and distinctly longer than the metatarsus, which is shorter than the rest of the tarsus. Length 2½ mm. . . . . **perturbans.**

Wing lanceolate; fork of second vein and that of fourth vein practically opposite one another. Colour of insect silver grey. Genitalia of male with the middle chaetae subapical. Hind femur nearly as long as its tibia, more than twice the length of the metatarsus, which is shorter than the rest of the tarsus. Length 1½ mm. . . . . **minutus.**

5. Fork of upper branch of second longitudinal vein barely before tip of first longitudinal vein (not a reliable character). Sides of thorax conspicuously paler than the dark dorsum. Genitalia of male with two chaetae at tip and three median ones.

Hind femur less than half as long as the tibia, distinctly shorter than the metatarsus, which is longer than the rest of the tarsus . . . . **argentipes.**

Fork of upper branch of second longitudinal vein some little distance before tip of first longitudinal vein. Thorax more uniformly concolourous **6**

6. Length 3 to 3¾ mm. Wings comparatively broad. Colour of insect grey. Genitalia of male with two chaetae at tip and three median ones . . . . **major.**

Length 2½ mm. Wings narrower or moderately broad **7**

7. Wings narrower. Colour of insect yellowish grey. Genitalia of male with three chaetae at tip and two median ones. Hind femur between one-half and three-quarters as long as the tibia, and nearly twice as long as the metatarsus, which is shorter than the rest of the tarsus . . . . . . **papatasi.**

Wings moderately broad. Colour of insect rather dark brown. Hind femur about half as long as its tibia; equally as long as the metatarsus, which is equal in length to the rest of the tarsus (the male is unknown) . . . . **argentipes,** variety **marginatus.**

8. Length 2½ mm. Wings purplish irridescent. Genitalia of male with four chaetae (2 apical, 1 subapical, 1 median) **malabaricus.**

Length 3 mm. Wings uniformly pale brownish grey. Genitalia of male with five chaetae (2 apical, 3 median) . . . . **zeylanicus.**

Phlebotomus himalayensis, Annandale. A yellowish grey species resembling *minutus* in general appearance, but distinctly larger and yellower; the wing is easily distinguished by the length of the anterior branch of the second longitudinal vein. It is found in the Himalayas between the altitudes of 4,000 and 7,000 feet, and is common during May, June and July.

Phlebotomus perturbans, Meijere. A dark brown species abundant in the jungle hills at the base of the Eastern Himalayas; it is also found in Java.

Phlebotomus minutus, Rondani. (*P. babu*, Annandale.) Probably the same as the European form, but according to Annandale it is of a silvery grey colour. It is the smallest of the Indian species, and can be distinguished from *argentipes* by its narrow wings and uniformly greyish colour. It is widely distributed all over India, and is common in Ceylon; but is not found at high attitudes. In Madras it is common in June and July, and sometimes in September, especially after small showers of rain, but it entirely disappears during the south-west monsoon and is never seen during the cold weather.

Phlebotomus argentipes, Annandale and Brunetti. Thorax dark brown or even blackish, sides yellowish, a character by which it can be easily distinguished from all the other Indian species. It is widely distributed along the east coast of India, and is also found in parts of Ceylon. Annandale states that it has the habit of biting the ankles under a dinner table. A variety of a lighter colour, named by him *marginatus,* is also said to occur in Ceylon.

Phlebotomus major, Annandale. Allied to *argentipes* but distinguished by its larger size, uniform golden colour, more elongate tarsi, and by the characters of the male genitalia. It is found all along the outer Himalayas from the base to 8,000 feet above sea level. A variety *grisea,* Annandale, is recorded from Kurseong in the Darjeeling district; it is greyish or brownish and not of a golden colour.

Phlebotomus malabaricus, Annandale. This species is closely related to *perturbans,* and is found in the jungles at the base of the Western Ghats.

Phlebotomus zeylanicus, Annandale. Thorax and abdomen brown. Wing venation characteristic, but resembling that of *malabaricus* and *himalayensis.* It is recorded from Peradenyia, Ceylon.

According to Annandale *P. papatasi* is widely distributed in North-West India, and is found as far east as Pusa in Bihar. In *Chritral* it has been associated by Wall with a form of fever resembling Phlebotomus Fever.

The following species are recorded from Africa :—

Phlebotomus duboscqui, Neveau-Lemaire. A species related to *papatasi* but differing in its darker colour, smaller size, and shorter proboscis. The antenna in the female is said to consist of thirteen segments—an unusual number in the genus—and the apical joint is shorter than the preceding one. Newstead appears to be doubtful as to whether it is distinct from *papatasi.* It is found in the French Soudan.

Phlebotomus antennatus, Newstead. This species can be distinguished from most of the other *Phlebotomi* by the structure of the antennal joints, which are short and stout, the third to the thirteenth being more bead-like than in the case of any of the other species. According to Newstead, it is distinguished from *P. minutus,* variety *africanus,* by its stouter and shorter legs. It is found at Salagoa on the Gold Coast.

Phlebotomus squamipleuris, Newstead. A small species, which may be mistaken for *P. papatasi,* but is distinguished from it by its narrower wing, and by the fact that the pleurae are clothed with large flat scales like those of mosquitoes. It is found at Khartoum in the Soudan.

South American species of Phlebotomus.

Lutz and Neiva, in a recent number of the Memoirs of the Oswaldo

Cruz Institute, have described the South American species of the genus *Phlebotomus*; most of them were taken in uninhabited regions, particularly in forests where bamboo-inhabiting mosquitoes were plentiful. For the determination of the species they note that the relative lengths of the segments of the palpi afford valuable taxonomic characters in both sexes. They give the following key to three species:—

1.	Scales absent on the abdomen	2
	Scales present on the abdomen between the hairs . . .	**squamiventris.**
2.	Last palpal joint longer than the others	**longipalpis.**
	Last palpal joint shorter than the second or third . . .	**intermedius.**

Phlebotomus rostrans, Summers. This species is distinguished from the above by the great length of its head and proboscis, which in the female, taken together, are half the length of the rest of the body. It is recorded from Rio Javary.

Bionomics

The bite of the sand fly is well known to everybody who has experienced it; the stealthy way in which it enters a mosquito net, either through the meshes, or by crawling under the curtain, or even by passing in between the mattress and the framework of the bed, make it a hated pest. The intolerable itching produced by the bite, and the stinging nature of the bite itself, are diagnostic of the presence of these flies. Some people, however, are in no way affected by it. The hands, the wrists, the dorsum of the feet, and the ankles are the favourite sites in which they bite; the face is also sometimes attacked. If a light is kept close to the bed fewer will enter the net.

According to Marett, *Phlebotomus* in Malta does not fly long distances, about twenty yards being the limit of range of flight. If a strong wind is blowing they are only seen in very small numbers, but when the wind dies down they reappear and their presence becomes very noticeable. During the daytime they are to be found in dark corners, among dark clothes, recesses in cupboards, behind pictures and similar places. The dark bathrooms of Indian houses are favourite resting places, where they will bite even in the middle of the day.

In Malta Newstead notes that certain places were heavily infected while in others hardly any flies could be found; the same has been observed in Madras, for some houses have large numbers, while others close by are entirely free. Newstead attributes this localization to some unknown conditions which favour the breeding of the flies.

In Malta Marett has found the flies resting in caves and embankments, and in cracks in walls where the surface pointing has fallen away, and where large crevices are left into which they can pass. The females are most active on still sultry nights, and then as they become replete with blood they cannot readily pass through the meshes of the ordinary mosquito netting. The males, if present, nearly always escape. When trying to catch one of these flies it will be noted that they make short leaps like the hop of a flea.

Only the females suck blood, but Marett notes that both sexes may be seen burying their mouth parts in organic matter. The same observer states he has seen female sand flies, replete with fresh blood, coming out of a hole in a wall, and suggests that they had probably fed on rats.

Early stages

The breeding grounds of any species of *Phlebotomus* are extremely difficult to locate. The small size of the larvae, their colour, and the places in which they are likely to be found, all increase the difficulties. It is interesting to read even Newstead's account of his efforts in this direction in Malta, in which he only found a few larvae after prolonged and repeated search. In spite of the difficulties the worker should always endeavour to locate the breeding grounds of any species of *Phlebotomus*, as all information will prove of the utmost value to other workers in the same field.

Grassi found the larvae of *P. papatasi* in all kinds of damp refuse in cellars, and particularly on the sides of drains where water splashes or trickles down. In Malta, Newstead found the larvae in caves, and in crevices and fissures under loose rocks where there was some damp earth; they were at some distance from the surface. They were also found low down near the foundations of stone walls, and on the under surfaces of stones. In all these places there was organic matter of all kinds, chiefly the excreta and remains of insects, wood lice, etc., as well as sufficient moisture and absence of light. It should be noted that, as Newstead points out, the larvae of *Phlebotomus* have the habit of flicking themselves off the surface of the stone or other object when exposed to light, and are easily lost. The pupae are the most difficult to detect, as their colour harmonizes with their surroundings.

Marett reports having found the larvae in wells, latrines, tanks, ventilation shafts and manholes, but the chief breeding places in Malta, according to this observer, are stone walls which are dry above ground level, but moist below the surface.

Howlett found larvae in the following situations at Pusa, Bengal:—

1. The nearly dried mud of a cement channel, leading from a well reservoir.

2. A small heap of kitchen refuse near the base of a wall.

3. The damp earth between some bricks, forming a small platform for a sacred plant in the courtyard of a house. The bricks in this case were more or less covered with algal growth, and among them were ants, the larvae and nymphs of wood lice, the larvae of Mycetophilidae, and other small creatures.

4. Among the bricks and tiles in a small heap of earth and rubbish, where the conditions were similar to those mentioned above.

5. The damp leafy matter taken from the earthy sides of an open reservoir where water from several gutters accumulated; the gutters, which led from houses, were of cement and contained much nitrogenous matter.

Howlett also suggests that in India the nests of termites may be places where sand flies breed, for the adult insects have been seen in the surface galleries.

Newstead has observed the method of oviposition of ***Phlebotomus*** in captivity, and notes that the fly assumes a curious attitude; it lowers its proboscis, crosses the middle and hind pair of legs behind the abdomen, which is then elevated and extended to the full; the egg is then shot out to a distance equal to about three times the length of the abdomen.

The *egg* (Plate XXXIII, fig. 1) is translucent when first laid, and is covered with a thin layer of viscous substance; five hours later it assumes its normal colour. Newstead describes it as follows:—'Form very elongate, dark brown, shining, with longitudinal black wavy lines, which in certain lights give the periphery of the egg a faintly rugose appearance; these black lines are slightly raised, and are joined by slender cross lines so that a faint but rather coarse reticulation is formed. The transverse lines are, however, very difficult to trace unless they are illuminated by a strong beam of light.' The incubation period lasts about nine days.

The *larva* (Plate XXXIII, fig. 3) is cylindrical and like a small caterpillar. It has a dark head, greyish white body, and long caudal bristles. The antenna consists of three segments, the two basal ones rudimentary, the third broad and flat, and armed with a centrally placed hair. It has black caudal bristles arranged in two pairs; each inner bristle is almost as long as the body, while the outer ones are shorter.

The pupa (Plate XXXIII, fig. 5) is ochreous buff, with a curved abdomen and a triangularly shaped head. The front view of the head resembles that of a ram in miniature, the long antennal sheaths, curving behind the eyes, simulating the horns. The larval skin, at least in ***P. papatasi***, is always attached to the two distal abdominal segments, a condition which is also seen in the larvae of some Chironomidae (*Forcipomyia*).

Breeding technique

In order to breed out *Phlebotomus* from the egg a number of replete females should be caught and kept in a large test tube together with some moist filter paper; the mouth of the tube should be covered with a piece of muslin and not with the ordinary mosquito netting. Males, if they can be caught, should be kept with the females and the tube placed in a cupboard. When the eggs are laid they should be transferred with the aid of a fine brush to some moist organic matter such as the remains of an insect; if they adhere too firmly to the filter paper, the piece should be cut out. It is sometimes possible to raise a few flies in this way, but the task is not an easy one and requires constant attention.

Marett has successfully bred out *P. papatasi* in a test tube on the sides and the bottom of which be placed the excreta of lizards and wood lice, first moistening it with water. After the flies had paired the females were transferred to the prepared test tubes, and were fed as soon as the previous meal had been digested. After the eggs were laid, the tubes were kept moist by daily adding a drop of water, and by wetting the cotton plug. The larvae hatched in from six to eight days, and were then transferred to a petri dish by filling the tube with water, which was then poured on to filter paper cut to fit the dish. The larvae float and later come to lie on the excreta. It is important to avoid an excess of moisture.

FAMILY CULICIDAE

Slender Nematocera *with either a long forwardly directed proboscis adapted for piercing in the female, or with a short proboscis. The head is small and spherical in shape; the eyes are reniform; ocelli wanting. The antenna is slender and is composed of fourteen or fifteen joints, the basal one being globular, and either bare or hairy; the remaining segments are covered with hairs; it is plumose in the male, and pilose in the female. The thorax may be arched, and there is no transverse suture. The scutellum is narrow, and may be unilobed or trilobed. The metanotum may be hidden, or visible, when it is usually arched. The abdomen is elongated and somewhat flattened, and is composed of eight or nine segments; the male genitalia are prominent, and the ovipositor is short. The legs are long and slender, the coxae comparatively short, the tarsi are elongated, and the claws toothed in the* *male, but rarely with more than two serrations. The wings are long and narrow, and when at rest folded flat on the abdomen; the venation is characteristic and constant; six longitudinal veins are nearly always present, the second, fourth and fifth are forked; the third is simple and arises from the anterior cross-vein about the middle of the wing; two basal cells are nearly always present. The veins are clothed with hairs or true scales, and the hind margin is fringed with scales or simple hairs.*

At present the family Culicidae contains about 1250 known species distributed all over the world.

Classification of the Culicidae

The Culicidae, like many of the other families of the Diptera, contains species which show minor differences in structure, the value of which is a matter of dispute. Dipterologists, however, have been content to recognize two subfamilies of the Culicidae, the Corethrinae in which the proboscis is soft and not armed for piercing, and the Culicinae in which it is long and is, at least in the female, armed for piercing.

The blood-sucking habit of the female mosquito, and the relation of certain species with the transmission of the parasites of malaria, yellow fever and filariasis, have stimulated the study of these insects, with the result that workers of all nationalities have collected them from all parts of the world. In order to facilitate this study and to make the work of others accessible, Theobald has written an exhaustive monograph of the group, in five volumes, classifying them according to the structure and position of the scales on the various parts of their bodies. In Volume I of his work, *The Culicidae of the World*, he recognizes six subfamilies of the Culicidae, of which the Corethrinae is one, and this grouping is retained in Volume III published in 1903. In 1905 Eysell published a paper in which he suggested the separation of the Corethrinae from the Culicidae, raising them to family rank; the family Culicidae being retained for mosquitoes alone. Theobald in Volume IV of his monograph, published in 1907, following this suggestion, divided the family Culicidae into ten subfamilies and more than one hundred genera, many of which are subdivisions of the older genera. In Volume V, published in 1910 he retains this classification but adds several new genera.

Dipterologists have taken exception to this classification. Williston, for instance, points out that scale characters are highly artificial, and that a genus of mosquitoes cannot be raised to family rank without raising all other genera of equal rank in a like manner. Whether the classification based on the characters of the scales, resulting as it has in the multiplication of genera, is a natural one or not it is impossible to say. Theobald maintains it is the best method of grouping these insects, as it is simple and can be used by medical men and others in determining the species in the field. It must be said, however, that culicidologists themselves do not appear to be agreed as to the species which belong to many of the genera.

The separation of the Corethrinae from the Culicidae is certainly a retrograde step, for although it is true that the former are devoid of a biting proboscis, in other respects, especially in venation, they agree exactly with the Culicinae. No better parallel example could be given than the Stomoxydinae, (*Stomoxys*, *Stygeromyia*, *Haematobia*, *Haematobosca*, *Bdellolarynx* and *Lyperosia*) in which the proboscis is very different from that of *Musca*, yet *Stomoxys* and *Musca* unquestionably belong to the family Muscidae, the two being linked together by the genus *Philaematomyia*. So also many of the Pangoninae, to take another example, have non-biting proboscides, yet they are placed by all dipterologists in the family Tabanidae.

According to Williston and others the Dixidae, which show many culicine affinities, should be included as a subfamily of the Culicidae, which is then constituted as follows :—

SYNOPSIS OF THE FAMILY CULICIDAE

Proboscis projecting somewhat, not adapted for piercing ; entire insect almost devoid of hair and scales, especially the antennae in both sexes . . . . subfamily	**Dixinae.**
Proboscis short, not adapted for piercing ; entire insect hairy, the antennae plumose in male and pilose in female . . . . subfamily	**Corethrinae.**
Proboscis much longer than the head, firm and well adapted for piercing in the female ; head, thorax, abdomen, legs and wings, except in some species, covered in parts or entirely with scales . . . . subfamily	**Culicinae.**

SUBFAMILY DIXINAE

Slender Nematocera, *almost devoid of hairs. Eyes round and dichoptic ; ocelli wanting. Antennae elongated, basal joint globular, the remainder of varying length and size, the terminal ones almost filiform ; palpi four-jointed. Thorax arched, without a transverse suture ; scutellum unilobed and transverse, metanotum arched. Abdomen long and slender, consisting of eight segments, pointed in the female, and* *thickened posteriorly in the male. Legs long and very delicate; tibiae without terminal spurs. Wings well developed; the subcostal vein ends about the middle of the wing; the second longitudinal arises from the first, also about the middle of the wing, and appears to be the commencement of the third vein; it then arches forwards, and divides into two; the fourth longitudinal vein is also forked. The seventh vein is rudimentary. There are four posterior cells, but the discal cell is absent.*

This group, the members of which are confined to the single genus *Dixa*, Meigen, can be recognized by their large wings, distinct and characteristic culicine-like venation, and their long filiform, almost bare antennae. They are usually treated as a family, and are regarded as being intermediate between the Tipulidae and the Culicidae. The character of the venation, the presence of the basal globular joint to the antenna, the larger size of the claws of the fore and mid-legs in the male, and their serration, are all points which link the Dixinae with the Culicinae.

Early stages

The larva of *Dixa* was studied by Reamur in 1714, and later by de Geer and Meinert, the latter depicting its structure in detail, as well as that of the pupa. The larva consists of twelve segments, and is bent at the fifth and sixth in the shape of a syphon, so that the head and anal end almost meet; in this characteristic attitude it rests at the surface of water. On the ventral surfaces of the fourth and fifth segments there is a pair of pseudopods armed with hooks, and on the eighth, ninth and tenth there are a number of stiff spines grouped together. There is a respiratory cup on the last segment, a terminal spine with three bristles, and two lateral processes armed with long or short hairs; in some species the fifth to the tenth segments inclusive are furnished with shields bearing spines. The larva is found in shady pools containing weeds and algae, and as it is often of a dark brown colour, it may be easily overlooked. The pupa, which is almost black, lies motionless at the surface of water with its abdomen bent up under its thorax. It has a pair of respiratory trumpets just behind the head.

Four species of *Dixa* have been described by Brunetti as occurring in the Himalayas; Adie records a species from Lahore.

SUBFAMILY CORETHRINAE

Slender Nematocera *with densely hairy bodies. Eyes kidney-shaped and dichoptic; ocelli wanting. Antennae long, markedly plumose in the* *male and pilose in the female; the first segment is globular. Palpi four-jointed and reclining downwards. Proboscis very short, concealed, and not formed for piercing. Thorax arched and projecting somewhat over the head. Scutellum simple, never lobed; metanotum arched. Abdomen long and slender, consisting of eight segments. Legs long and delicate, always hairy, and tibiae without spurs. Wing venation typically culicine, scales only present on the wing fringe, and a few of the veins, otherwise the wing surface is hairy.*

The genera of the Corethrinae may be recognized by the following table modified from Williston's key:—

1.	Metatarsus shorter than the following segment	**Corethra (Mochlonyx).**
	Metatarsus longer than the following segment	2
2.	Large species (10 mm. or more long) with true scales on cross-veins and with bifid claws	**Pelorempis.**
	Small species, claws simple	3 or 4
3.	Antennae with second segment long, spaces between verticils bare, true scales on distal parts of veins	**Ramcla.**
	Antennae verticillate, veins devoid of scales, and only clothed with hairs	**Chaoborus. (Sayomyia).**
4.	Antennae with second segment long, spaces between verticils hairy	**Corethrella.**
	Antennae with second segment short, spaces between verticils bare	**Eucorethra.**

There appears to be some confusion regarding the synonomy of the Corethrinae. The species which Lichtenstein (1800) named *Chaoborus antisepticus* was only described in its larval stage, and it remains an open question as to whether it was a true *Corethra* (*C. plumicornis*) or not; in any case, it seems a pity to change the well established and familiar name Corethrinae to Chaoborinae, as has recently been suggested by Edwards.

Early stages.

The larva of *Corethra* is common in pools and ponds in Europe, and is a well-known natural history object; it is almost transparent, and has been aptly named the 'Phantom larva'. It lies horizontally extended on the surface of the water, now and then suddenly whisking its posterior end and darting after its prey, for it is predaceous. Its head is pointed anteriorly; antennae project over its mouth, and are armed at their extremities with five long curved bristles. When not in use they are flexed on the basal joint. The labrum is long and keel-shaped, and the mandibles are armed with several strong teeth. It preys chiefly on small larvae, which are caught by the antennae and crushed between the mandibles. The larva has no stigmata; the tracheal tubes have, however, two pairs of air sacs, one in the thorax and the other towards the end of the abdomen, which act as floats, and keep the larva suspended horizontally. The last abdominal segment is armed on its ventral surface with a vertical fin, which bears a row of feathered bristles. The pupa floats in an upright position at the surface of water, and has a pair of trumpets on its thorax, not unlike those of the culicine pupa. The end of the abdomen is armed with a pair of broad fins, by which the larva propels itself.

Annandale has recently described the larva, pupa, and imago (male) of a small gnat, *Ramcia inepta*, from Peridenyia (4,300 feet), Ceylon. Although the fly has a short proboscis, it has a striking culcinae affinity in that its veins are partly covered with true scales. The larva, which was found in a swamp, is said to resemble somewhat that of the culicid genus *Stegomyia*; it has a broad triangular head, long jaw-like antennae, and distinct thoracic segmentation; floats and fins are entirely wanting.

Annandale considers that *Ramcia inepta* is more closely related to the Corethrinae than the Culicinae, but that it links the two groups together.

SUBFAMILY CULICINAE

Long slender Nematocera, *clothed with characteristic scales. Eyes kidney-shaped and dichoptic; ocelli absent. Antenna long, with fourteen segments in the female, and fifteen in the male, always pilose in the former and plumose in the latter. Palpi four-jointed, either long or short in both sexes, or short in one and long in the other; if short they are nearly always straight. Proboscis long and in the female armed for piercing, for the majority of* mosquitoes *are true blood-sucking insects; in the male it is simple, and is never used for piercing. Scutellum may be simple, consisting of one lobe, or it may be trilobed, and furnished with scales or hairs; metanotum as a rule well developed, and often covered with scales and hairs. Abdomen long aud slender, consisting of nine segments, and for the most part covered with scales and hairs, especially in the male. Female genitalia consisting of two spatulate lateral lobes, covered with scales or hairs. Male genitalia composed of two claspers, each with a large basal lobe, and a variously shaped terminal knee-like joint; at the apex of the basal segment there is often a well developed spur or spine, which may sometimes be bifid. On the ventral surface of the claspers there is often* *a lobed structure, consisting of one or more spined tubercles, or a long acutely hooked process at the apex of the basal lobe. Arising from the base of the claspers are the harpes, which are of very varied structure, but usually consist of a long blade-like piece of chitin. There is also a pair of smaller claspers, usually formed of stout, recurved hooks which lie above the harpes. In some species there are processes on the ventral margin armed with strong teeth, which are spoken of as the unci. Veins of the wings clothed with scales of various kinds, the membrane between them being hairy; light or dark scales are often present in patches, thus forming the characteristic light or dark spots seen on the wing of Anopheles. The fringe is bordered with scales of various kinds. The venation is characterisitc and as follows:—The costal vein borders the entire wing, and the subcostal joins it nearer the apex than the base; the first longitudinal curves outwards, and on turning slightly downwards, ends just above the tip of the wing; the second longitudinal vein is forked, the forks ending at the apex of the wing, and enclosing the first submarginal cell; the third longitudinal vein is simple and straight, and is united to the veins above and below it by the supernumerary* and mid-cross veins* (Theobald)*; the third vein ends just below the tip of the wing. The fourth vein is forked, the forks enclosing the second posterior cell. The fifth vein gives off an anterior branch, halfway down its course, and the forks thus formed enclose the fourth posterior cell; the anterior branch is joined to the fourth vein by the posterior cross-vein. The sixth vein is simple and somewhat curved. When at rest the wings are folded over the abdomen. The legs are long and slender, the hind metatarsus is usually long; the claws are equal and small in the female, and may or may not be serrated; in the male those of the fore and mid legs are unequal and serrated, but rarely with more than two serrations; the hind claws are always equal.*

The subfamily Culicinae at the present time contains some 1,200 species, and this number is being added to almost every month. A large proportion of the females are blood-suckers, but many never bite, and like the males, subsist on plant and similar juices.

It has already been pointed out that the elaborate classification of Theobald has for its basis the structure and arrangement of the scales, which clothe the bodies and wings of mosquitoes, so that before taking up the consideration of the genera and species it will be convenient to describe some of the common types of scales met with.

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* The supernumerary cross-vein is considered by some dipterologists to be the basal section of the third long vein, and not a true cross-vein; the mid cross-vein is also spoken of as the anterior cross-vein (see page 80).

Mosquito Scales (Plate XXXV)

A true scale can be recognized by its ribbed appearance, the ribs simulating the veins of the wing of an insect in miniature. It is nearly always attached by a delicate stalk, which is often bifid. Its free end may either be flat with minute serrations, or convex with projecting sides; or sloping gently to a blunt point. On the head of a mosquito there are, as a rule, three types of scales to be seen. 1. Upright curved scales. 2. Upright forked scales. 3. Broad flat scales which are closely applied to the surface. All the three types of scales are found on the vertex, and they exhibit great variation in colour.

On the thorax there are commonly four types of scales in addition to hairs. 1. Upright curved scales, found all over the thorax and scutellum. 2. Spindle-shaped recumbent scales, varying in size, and scattered irregularly over the surface. 3. Flat scales similar to those on the head, and found chiefly on the scutellum and just below the roots of the wings. 4. Long narrow twisted scales, well marked in the mosquitoes of the *Mucidus* group.

The scales on the abdomen are best seen in the culicine mosquitoes, in which they form a dense covering, and are broad and flat; most of the anophelines have none of these scales, but a few are seen in some species, either forming tufts at the sides of the segments, or scattered irregularly at the lower end of the abdomen and on the external genitalia.

The veins of the wing are clothed with a double row of somewhat broadly expanded flat scales, and in addition there are often lateral ones of varying shape, some long and straight, others curved. In some mosquitoes the scales on the wings are more or less ovate, the apical border being convex. The wing fringe has two types of scales, one short, the other longer; there are also small border scales, which are flat and narrow.

The legs are always covered with flat scales and hairs, and in some species they are greatly exaggerated, and project from the surface.

The worker will find that any species of *Culex*, *Stegomyia*, or *Anopheles* will provide almost all the varieties of scales which are likely to be met with.

The *eggs* of mosquitoes are laid on water, or on any vegetable matter lying on its surface; they may either be deposited singly or in a mass, adhering closely together. Most species of the genus *Culex*, while

PLATE XXXIV.

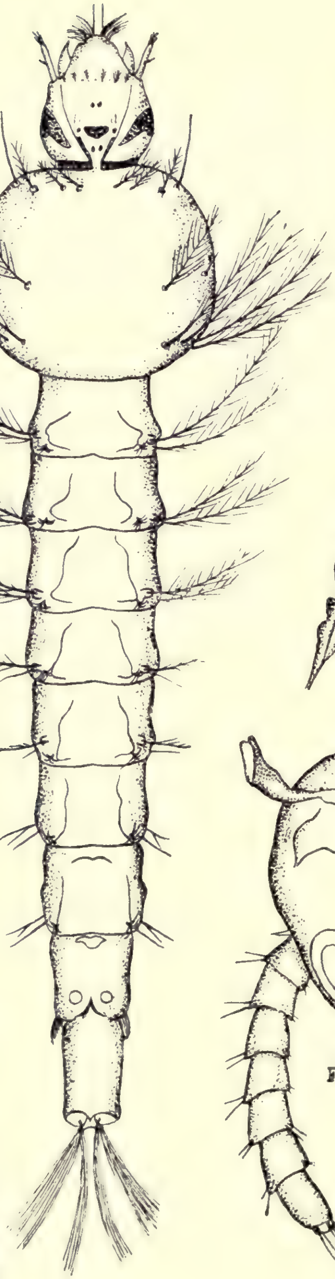

Fig. 1.

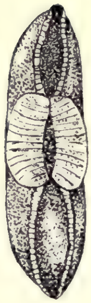

Fig. 2.

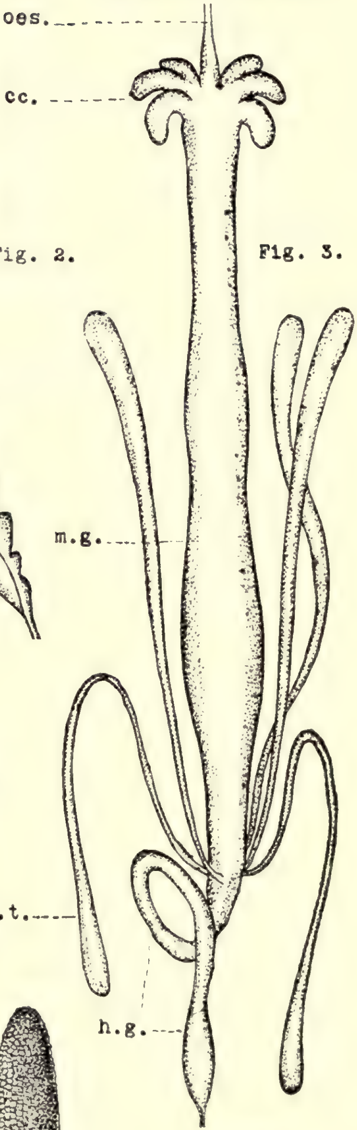
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Fig. 3.

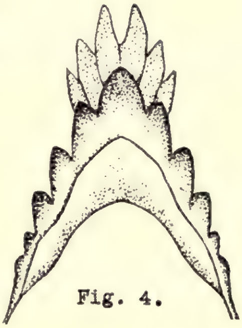

Fig. 4.

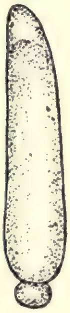

Fig. 5.

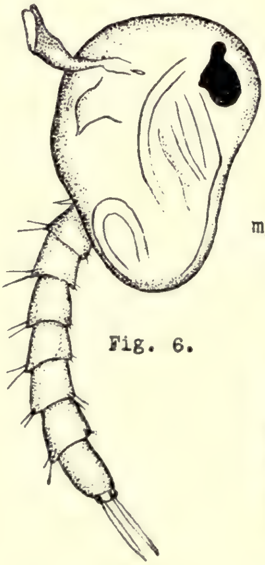

Fig. 6.

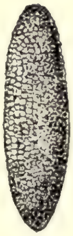

Fig. 7.

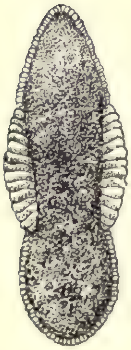

Fig. 8.

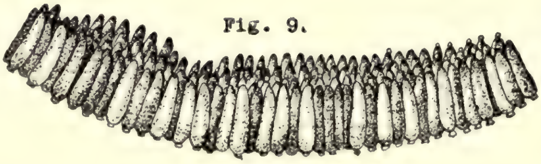

Fig. 9.

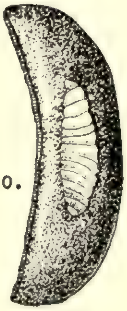

Fig. 10.

PLATE XXXIV

Figure 1. Larva of *Anopheles rossii*. × 30.

Figure 2. Egg of *Anopheles stephensi*. × 100.

Figure 3. Alimentary tract of larva of *Culex concolor*. oes., oesophagus. cc., coeca. m.g., mid-gut. mp.t., Malpighian tube. h.g., hind-gut.

Figure 4. Mental plate of larva of *Anopheles rossii*.

Figure 5. Egg of *Culex fatigans*. × 120 about.

Figure 6. Pupa of *Anopheles rossii*. × 15.

Figure 7. Egg of *Stegomyia sugens*. × 100.

Figure 8. Egg of *Anopheles fuliginosus*. × 100.

Figure 9. Egg raft of *Culex fatigans*. × 22.

Figure 10 Egg of *Anopheles culicifacies*. × 100.

Early stages. The eggs. (Plates XXXIV and XXXV)

depositing the eggs collect them together into a regularly arranged heap the so-called *egg raft*. The female in doing so crosses her hind legs arranging each egg as it is passed out. The egg mass of *Culex fatigaus* (Plate XXXIV, fig. 9) is a typical example of this kind of egg raft; it is boat-shaped and consists of from 200 to 400 eggs.

The egg (Plate XXXIV, fig. 5) is an elongated ovoid, broadly rounded off at the end which lies on the surface film of the water, and which has attached to it a delicate globular process, the *micropilar apparatus*. The larva escapes from the broad end, and is thus able to dive straight into the water. When first laid the eggs are white, but they soon become dark grey. The individual eggs can be readily separated, and the whole mass breaks up when the larvae hatch out.

Many culicines lay their eggs singly, depositing them irregularly on the surface of the water, or at its margin. The eggs of these species show great structural variation. Some are long and pointed, as those of *Mansonia* and *Panoplites*; in *Megarhinus* they are club-shaped, while in others they are either spindle-shaped or oval. The eggs of *Stegomyia* (Plate XXXIV, fig. 7) are surrounded by a frill containing air, and in *Janthinosoma* they are covered with minute spines.

The eggs of *Anopheles* (Plate XXXIV, figs. 2, 8 and 10), which are also laid separately, are characteristic, being as a general rule boat-shaped; the upper surface is flattened in the transverse diameter, and is surrounded by a delicate striated rim or frill. One end of the egg is usually broader than the other. Attached to the sides of the egg are the *floats*, which are small ribbed structures containing air; they are present on the majority of anopheline eggs, though there are some remarkable exceptions. Stephens and Christophers have drawn attention to the variation in the shape and position of the floats, and in the width and extent of the frill on the upper surface. They have thus been able to distinguish the eggs of most of the Indian anophelines.

When examining the egg of an *Anopheles* it is important to note the character of the frill, whether it is broad or narrow, and whether the floats encroach on it. The size and position of the floats should also be noted, as well as any other special markings on the surface of the egg.

The body of the culicid larva shows a greater resemblance to the adult than is usually the case in the Diptera, being divided into head, thorax and abdomen. In their general structure the larvae of the

Culicinae conform to a common type, of which, however, there are characteristic modifications in the different genera. Dyar and Knab have used the characters of the larvae as a basis for the classification of the Culicinae, and though there is at present no general agreement regarding the value of such larval characters, it is often a matter of practical importance to be able to recognize species in their larval stage. Even the most minute details of the external anatomy are, therefore, worthy of attention.

External structure of the larva

As it is in the anopheline mosquitoes that differentiation is the most important, *Anopheles rossii* will be taken as a type, the special characters which are of use in separating species in this genus being emphasized. The modifications found in the Culicina will be referred to subsequently.

The head and its appendages

The *head* of the larva of *A. rossii* is roughly spherical, slightly flattened in the dorso-ventral diameter, and narrowed in its anterior third, from the point of the insertion of the antennae. The posterior border is slightly constricted, and is encircled by a collar-like rim of pigmented chitin, continuous except at the middle line dorsally, where there is a slight interval. From this point a V-shaped suture passes forwards, the two arms diverging to extend to the inner side of the base of the antenna. In the angle between the two limbs there are several symmetrically arranged patches of dark brown pigment, forming a pattern which, although subject to slight variation, is characteristic of the species. The dorsal surface slopes rather sharply to the distal border of the head, where it terminates in a slightly thickened transverse bar, termed by some writers the clypeus, by others the labrum. Arising from, or slightly behind, this border there are two pairs of hairs, termed the *clypeal* or *frontal hairs*. The external pair of these project forward on each side over the feeding brushes, and are on this account not always easy to distinguish. The internal hair is set nearer the edge, and projects in the interval between the feeding brushes. In *rossii* both these hairs are simple and unbranched*, but in other species they may be forked or branched forming a complete cockade, thus affording a valuable distinguishing feature. About the middle of the head there is on the dorsal surface an arched transverse row of six large feathered hairs, all of which project upwards and forwards, reaching as far as the distal border of the head. Behind these, and on each side of the pigment spots between the arms of the V-shaped suture, there is another row of four smaller hairs, and further back a pair of small simple hairs.

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* A hair is said to be *branched* when the branches lie in more than one plane, and *feathered* when all are in one plane (Nuttall and Shipley).

The *antennae* arise from the sides of the head a little in front of its middle point. They are generally described as two-jointed, the basal joint being fused with the head wall. The projecting portion in *rossii* is a simple cylindrical and tapering organ, usually directed forwards, but capable of movement in a lateral direction. Its surface is sparsely covered with short recumbent hairs, and at the distal end there are two short spines, projecting from a papilla which is probably sensory in function. In many species there is a plume of hairs on one side of the antenna, inserted at varying distances from the base, and known as the *basal tuft*. This is represented in *rossii* by a single short hair, easily overlooked if the side on which it lies happens to be away from the observer. The terminal portion at the base of the papilla may also bear hairs, those found in this situation being usually shorter and stouter than the proximal ones. The papilla itself may be lengthened—though not in *Anopheles*—to form a distal joint.

The *eyes* vary a good deal according to the age of the larva, as both the primitive larval eye and the early stages of the developing eye of the adult are present. The former is seen as a round or oval patch of pigment situated behind the insertion of the antenna, while the compound eye appears as a collection of isolated pigment spots slightly dorsal to this; they often show a crescentic outline.

The ventral surface of the head is more irregular than the dorsal, a considerable part of the anterior area being occupied by the mouth parts. There is a median longitudinal suture extending forwards from the collar, and a lateral suture some distance on each side of this.

The mouth is adapted for the ingestion of minute particles, and is provided with an apparatus for setting up a current in the water to attract them, the larva remaining stationary or at the most turning round in a circle as it feeds; the particles are entangled in a sieve-like arrangement of hairs, the water being discarded and the food swallowed. The structures which form the mouth are the feeding brushes and certain accessory bunches of hairs, the mandibles and first maxillae, and the mental plate, with which is connected the hypopharynx.

The *feeding brushes* are dense masses of long fine hairs, set one on each side of the distal end of the head. Each is attached to a thickened ridge of chitin at the side of the ventral margin, and is provided with two muscles, by means of which it can be rotated inwards, and at the same time retracted within the oral cavity. In the resting position the bunches of hairs are spread out and project well in front of the clypeus; they do not present any special modifications of taxonomic value. In predaceous larvae the hairs are much fewer in number, and are much stouter, and may be serrated; such larvae use their feeding brushes in seizing their prey. (James.)

Between the feeding brushes, in the middle of the ventral margin, there is a bunch of seven stouter hairs, directed forwards like a plume. These move with the feeding brushes, as they arise from the same membrane as that in which the apodemes of the latter are developed.

The Mandibles and Maxillae

The *mandibles* (Plate XXXV, fig. 1) are stout, somewhat quadrilateral appendages, consisting of a single joint, the two forming the lateral boundaries of the mouth aperture. The anterior and inner angle is armed with a set of dark brown chitinous teeth, apparently of little use in most anopheline larvae, which are surface feeders. On the anterior and external angle there is a group of four strong curved hairs, bent inwards over the teeth; these are used in cleaning the brushes. On the internal border there is a fringe of fine hairs, those of the two sides meeting when the mandibles are folded inwards. In the normal resting position the teeth of the mandibles lie near one another and immediately in front of the mental plate. They can be rotated outwards on their posterior and external angles through an angle of 90° or so.

The *maxillae* (Plate XXXV, fig. 4) are partly covered by the mandibles, and are neither easy to see when in *sitû* nor to dissect out. Each consists of a flattened and irregular chitinous plate, covered with fine stiff hairs which are mainly directed towards the anterior and internal angle, and are used, like those of the mandibles, in cleaning the feeding brushes. On the outer side of the maxilla there is a small spindle-shaped palp, the distal end of which is surmounted by three small stout spines, connected together by a membrane. The palp lies internal to the antenna, and is the most conspicuous part of the appendage. Neither mandibles nor maxillae afford useful distinguishing characters. The maxillary palp is small in most species of *Culex* and *Stegomyia*.

The *mental plate* (Plate XXXIV, fig. 4) lies in the middle line, at the posterior end of the mouth area, and between the two mandibles. It is small, triangular, and heavily pigmented, having its apex pointed and directed forwards, and its sides divided into a number of coarse serrations. This structure probably represents the rudiments of two fused maxillae, and is indeed termed the labial plate by some writers; others have pointed out its correspondence with the mentum of other larvae. In reality the

PLATE XXXV

Figure 1. Mandible of larva of *Anopheles rossii.*
Figure 2. Upright forked scale, after Theobald.
Figure 3. Upright forked scale, after Theobald.
Figure 4. Maxilla of larva of *Anopheles rossii.*
Figure 5. Twisted upright scale, after Theobald.
Figure 6. Broad wing scale from *Panoplites*, after Theobald.
Figure 7. Inflated parti-coloured scale, after Theobald.
Figure 8. Broad wing scale from *Aedeomyia*, after Theobald.
Figure 9. Small spindle-shaped scale, after Theobald.
Figure 10. Curved hair-like scale, after Theobald.
Figure 11. Flat spindle-shaped scale, after Theobald.
Figure 12. Narrow curved scale, after Theobald.
Figure 13. Flat scale from abdomen, after Theobald.
Figure 14. Spine from syphon tube of *Culex* larva.
Figure 15. Syphon tube and 8th and 9th abdominal segments of larva of *Stegomyia sugens.*
Figure 16. Syphon tube and 8th and 9th abdominal segments of larva of *Culex fatigans.*
Figure 17. Palmate hairs of larva of *Anopheles rossii.*

PLATE XXXV.

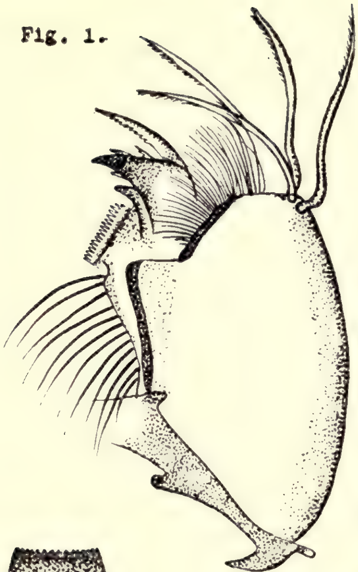


Fig. 1.

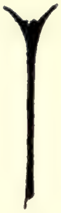
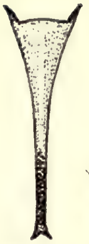


Fig. 2.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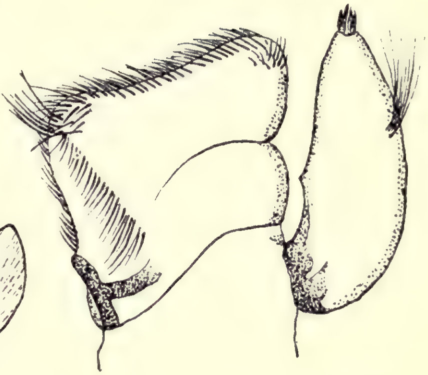
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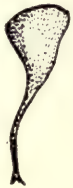
Fig. 5.

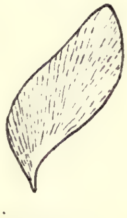
Fig. 6.

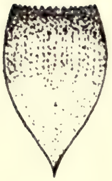
Fig. 7.

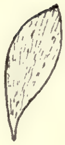
Fig. 8.

Fig. 9.

Fig. 10.

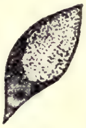
Fig. 11.

Fig. 12.

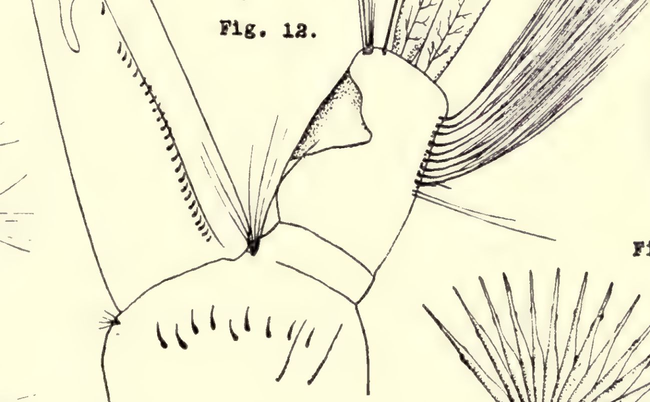

Fig. 15.

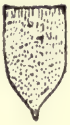
Fig. 13.

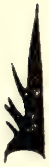
Fig. 14.

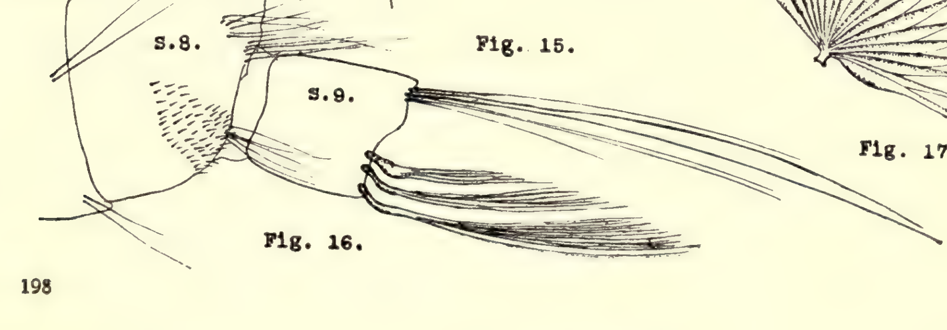

Fig. 16.

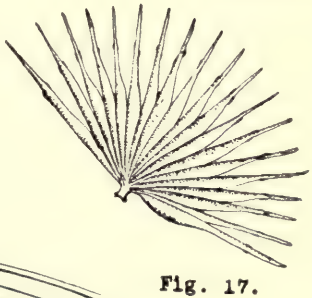
Fig. 17.

plate consists of two parts, one lying dorsal to the other, so that they appear as one when seen from above. The upper of these would correspond to the mentum, which has become displaced backwards behind the submentum. The salivary duct traverses the median area and opens at its tip.

The larva of *Anopheles* is a surface feeder, and therefore assumes an attitude parallel with the surface, retaining its position by means of the palmate hairs on the abdomen. The head can be rotated through an angle of 180°, so that the ventral surface becomes dorsal. The feeding brushes are moved rapidly inwards, and at the same time retracted, a succession of these movements setting up a current which carries any solid particles within reach towards the mouth. They are then secured and swallowed, while the water is allowed to escape. From time to time the stout hairs on the mandibles, and the shorter hairs on the maxillae, are used to remove the particles from the brushes, and to rearrange them.

Thorax and abdomen

The *thorax*, like that of the adult, does not show any clear divisions into segments. It is rounded in shape, and bears on its dorsal and lateral surfaces three rows of feathered hairs. The most anterior of these is situated at the front margin, and consists of six hairs which overhang the head. The second row lies a little behind the first, while the third, which consists of larger hairs than the preceding, is placed at the junction of the middle with the anterior third. The thorax is relatively much larger in adult than in young larvae, and in some species of *Anopheles* it may be furnished with palmate hairs, like those on the abdomen, to be described presently.

The *abdomen* consists of nine segments, diminishing gradually in size from before backwards. The first seven resemble one another, and are broadest in the transverse diameter; the eighth bears the respiratory opening, and the ninth the anus, with certain special structures. Each of the first three segments is furnished with a pair of long feathered hairs, directed forwards and outwards, and inserted on slightly raised areas at the lateral borders. The remaining segments are armed with simple hairs, and there are on each segment several smaller ones, as well as on the raised lateral areas. None of the structures afford reliable distinguishing characters.

Palmate hairs

The *palmate hairs* (Plate XXXV, fig. 17) are minute but elaborate structures, by means of which the larva is enabled to cling to the surface film. They are situated on the lateral part of the dorsal surface of the abdominal segments, and are peculiar to the Anophelina. The number varies in different species;

they may be present on all the abdominal segments, as well as on the thorax, or they may be confined to the more posterior segments. Each palmate hair consists of a number of delicate leaflets arising from a common stalk, and arranged in a radiating manner like the ribs of a half-opened umbrella. The basal portion of each leaflet is broad, and often appears concave, while the distal portion is usually narrowed and pointed. The edges of the leaflets may be notched in a characteristic manner. In *rossii* there is a small notch on one border. The number—nineteen in this species—and shape of the leaflet, are of specific importance.

Respiratory opening

The eighth segment bears the respiratory openings or stigmata, the terminations of the large lateral tracheae which traverse the whole length of the larva. These lie in the anterior part of an irregularly quadrilateral area on the dorsal surface. This area is raised a little above the level of the preceding segment, and is supported by a chitinous arch, the lateral arms of which are provided with a series of spine-like teeth, corresponding to the 'comb' of the larva of *Culex*. The anterior and lateral margins of the space in which the stigmata lie can be turned inwards so as to partly arch over the area, or again retracted when the larva is breathing. The raised portion is pushed through the surface film during respiration, so that the tracheae are in free communication with the air through the openings of the stigmata. When the larva sinks to the bottom, the openings are closed by the arching over of the sides of the area.

The ninth segment is narrower and rounder than the rest, and is a little elongated. Its dorsal border is furnished with two pairs of long feathered hairs, which are directed backwards as a tail. The ventral surface bears two rows of feathered hairs, arising in the middle line from an elongated and raised area of thicker chitin. The two rows are set very close together, so that when examined in side view they appear as one, and hang down at a right angle to the long axis of the body as a sort of fin; each hair is articulated into a little round pit in the chitinized area. Between the dorsal and ventral sets of hairs there are four similar and symmetrically arranged papillae. These are delicate transparent leaf-like structures, possessing a considerable amount of retractility. They are small in *Anopheles*, as it is a surface feeder, but become of considerable size in those larvae, such as some species of *Stegomyia*, which feed almost exclusively at the bottom of the water. These organs are invaginations of the body wall, and, as they contain blood, function as tracheal gills.

Syphon tube (Plate XXXV, figs. 15 and 16)

In all culicid larvae other than *Anopheles* the openings of the tracheae lies at the end of a tube of chitin of varying length, known as the *syphon.* This has the form of a cylinder, arising from the dorsal surface of the eighth segment, and usually narrowing a little towards the distal end. The apex is closed by a series of finger-like flaps of chitin, which can be opened when the larva ascends to the surface to breathe. At the base there is a thickened ring by which the syphon is attached to the eighth segment, and it is at this point that the tube, as a rule, attains its greatest breadth.

Christophers regards the shape of the syphon tube as a point of considerable taxonomic value, and has used as a taxonomic character the 'syphonic index,' obtained by dividing the length of the tube by its greatest breadth. The tube may be short and stout, or it may be of extraordinary length and very narrow. It may be furnished with several branched or simple hairs. On each side there is a row of peculiar spines, the number of which is important; these may be arranged in a regular row, or the row may be interrupted. At the base of the syphon, on the dorsal surface of the eighth segment, there is a row of spines representing the comb which surrounds the respiratory opening in *Anopheles.*

Apart from the presence of the syphon tube, there are many minor differences between the larvae of different genera. The head, for instance, is larger in *Culex* than in *Anopheles,* while in *Stegomyia* both head and thorax are relatively small. The antennae in *Stegomyia* are small and degraded, and have no small recumbent hairs, while the papilla is often well developed. In the genus *Culex* the antenna may show great variation. Striking deviations from the type are to be found in cannibal larvae, such as that of *Culex concolor.* In this species the syphon tube is short, and the larvae, therefore, either float almost horizontally on the surface or with their heads a little below it; in this position they remain stationary, waiting for their prey. The feeding brushes, as already noted, are transformed into clasping organs, and the clypeus is concave instead of straight.

The differences between the larvae of species even in well established genera are so great that they cannot be profitably discussed here. The character of each species with which the worker is concerned should be determined by an actual examination of the living larva between a slide and cover glass, and the specimens subsequently bred out and identified, the larval skin being retained for reference. The points which are of special importance are the presence or absence of hairs or spines on the antennae, the shape and number of the teeth on the mental plate, the syphonic index, the number of spines on the syphon tube, and in the comb at its base. It is particularly important to note whether the larva is carnivorous or not; if it is it must be bred with a known species with which it cannot be mistaken. The worker should be careful to compare only larvae of approximately the same size and age, as the later stages differ from the early one in some particulars. The hairs are generally more numerous and more branched in the full grown larva than in young specimens.

Internal structure of the larva

The *alimentary tract* of the larva (Plate XXXIV, fig. 3) is a simple one, and when dissected out is only a little longer than the body. The mouth leads into an oval or roughly quadrilateral pharynx, actuated by a complex musculature, which is situated in the middle of the head, and can be seen through the integument in living larvae. The oesophagus is a short and narrow tube passing through the neck, with a large amount of muscular tissue in its walls, mainly arranged in circular fibres. In the thorax it becomes continuous with the first part of the mesenteron. The junction between the two is effected in very much the same way as in the adult *Philaematomyia* already described, the end of the oesophagus being invaginated into the commencement of the mesenteron so as to produce a valve. The space between the two walls of the invaginated portion is a considerable one, and is probably, according to Imms, a blood sinus. Immediately below the valve there are eight coeca; these are short but broad sacs, constricted in the middle, the set being arranged in a regular row around the entrance to the mid-gut. The cells of the coeca secrete a granular material which is excreted into the lumen; they stain very deeply with haematoxylin. The mid-gut extends as far as the eighth segment, and is the same shape as the cavity in which it lies, and is not convoluted. Its wall is lined with a secreting epithelium similar to that in the adult insect. There is in the larva, however, a well developed peritrophic membrane. There are five rather short and stout Malpighian tubes, both in the larva of *Culex* and *Anopheles*. The hind-gut consists of a short and narrow ileum, well supplied with circular muscle fibres, and a wider pear-shaped portion, the colon, with which is included the rectum. There are no rectal papillae, these being probably represented by the external tracheal gills. The wall of the hind-gut has a well marked chitinous intima.

Many mosquitoes are naturally infected with flagellates of the genera

Herpetomonas and *Crithidia*, and the hind-guts of their larvae are the chief situations in which the parasites undergo their early development; in an infected larva they may be seen in large numbers massed together in the form of a palisade along the epithelial lining.

The pupa (Plate XXXIV, fig. 6)

Mosquito larvae moult three times, completely shedding their skins before they are ready to pupate; the organs of the imago commence to form during the last larval stage. The *pupa* emerges through a slit on the dorsal surface. Its appearance is very characteristic; it consists of a rounded body composed of the head and thorax, and an elongated abdomen flattened dorso-ventrally, and held underneath the body. The bulbous portion is enclosed in a delicate cuticle, through which the appendages of the developing imago can be readily made out. The antennae appear as lateral ridges arising above and in front of the compound eyes; they pass backwards over the legs to end in front of the wings. Arising from the dorsum of the thorax there are two stout tubes, the *respiratory trumpets*. These are constricted at their attached ends, but expanded distally, opening to the exterior by a V-shaped slit, which is directed inwards and guarded by a number of delicate hairs; the narrow ends of the trumpets are continuous with the lateral tracheae. Christophers has pointed out that the shape of the slit and the manner in which the trumpets project from the thorax are of generic significance. In *Anopheles* the trumpets are short and arise from the middle of the dorsum of the thorax, and have truncated ends; in *Culex* they arise from the posterior part of the thorax, are long and narrow, and the opening is somewhat oblique, while in *Stegomyia* the tubes are short and broad, and the openings triangular in shape.

The abdomen of the pupa consists of nine segments, the first of which is not clearly seen; its dorsal plate appears as a wedge between the base of the wings. The second segment and the remaining six are flattened dorso-ventrally; each dorsal plate is well developed, covering almost the entire segment, and its sides are thickened and furnished with posteriorly directed hairs. The eighth segment is armed with two large chitinous flaps, the *fins*, each being supported by a stiff bar which runs horizontally across to end in a hair at the free margin. The ninth segment has a pair of blunt processes lying between and in front of the fins; in the male they form a broad heart-shaped protuberance; in the female they are smaller, and thus afford a means of distinguishing the sex of the future imago.

The pupa of *Anopheles* is elongated antero-posteriorly, and as a rule hangs in the water in a much less vertical position than that of *Culex*, which is not so much elongated.

As the pupa increases in age additional hairs are developed and its body becomes darker in colour. Just before the fly emerges it comes to rest, and extends its abdomen; the dorsum of the thorax now splits, and the adult insect slowly extricates itself. As a rule the pupal stage lasts from three to four days, according to the temperature; it may be as short as forty-eight hours and as long as ten days.

James and Liston's Key to the identification of the known larvae of Indian Anopheles.

1. Antennae with a large branched hair
   - A. With simple unbranched frontal hairs . . . . . **lindesayi.**
   - B. With branched frontal hairs.
     - 1. Median frontal hairs unbranched. The branches of the external frontal hairs arise from the main stem and from other branches . . . . **barbirostris.**
     - 2. Median frontal hair unbranched. The branches of the external frontal hairs arise from the main stem only. **sinensis.**
2. Antennae without a large branched hair.
   - A. With fully developed palmate hairs on the thorax.
     - (*a*) With simple unbranched frontal hairs.
       - 1. The filaments of the palmate hair leaflets rather long. . **culicifacies.**
       - 2. Palmate hairs very large on thorax. Filaments shorter. Characteristic head pattern . . . . . . **listoni.**
       - 3. Basal hairs characteristic . . . . **culiciformis.**
     - (*b*) With branched frontal hairs.
       - 1. Two branched posterior hairs in addition to the frontal hairs. Palmate hairs large. Filament short . **jeyporiensis.**
       - 2. No posterior hair . . . . **maculipalpis.**
   - B. Without fully developed palmate hairs on the thorax.
     - (*a*) With simple unbranched frontal hairs.
       - 1. Characteristic head pattern. Filaments of leaflets long. **rossii.**
       - 2. No head pattern. Filaments shorter . . . . **stephensi.**
       - 3. Filaments very short and blunt . . . . . . **theobaldi.**
       - 4. Filaments short, sharp-pointed . . . . . . **maculatus.**
       - 5. Two long unbranched posterior hairs. Palmate hairs only on the last few abdominal segments . . **turkhudi.**
     - (*b*) With branched frontal hairs.
       - 1. Frontal hairs much branched . . . . . . **fuliginosus.**
       - 2. Frontal hairs only slightly branched or frayed . . **pulcherrimus.**
       - 3. External frontal hairs unbranched, median forked . **aitkeni.**

Edward's Key to the known larvae of African Anopheles.

1. Shaft of antenna with hair-tuft; no plumose hairs in middle of thorax overlapping occiput . . . . . **mauritianus.**

	Shaft of antenna without hair-tuft; plumose hairs present in middle of thorax in front	2
2.	Rudimentary palmate hairs on thorax	3
	Palmate hairs of thorax altogether wanting	6
3.	External anterior frontal hair much branched, forming a pronounced tuft	**squamosus;** **pharoensis.**
	External anterior frontal hair simple or slightly branched	4
4.	Posterior and internal anterior frontal hairs simple	**funestus.**
	Posterior and internal anterior frontal hairs branched	5
5.	Dark brown; filaments of palmate hairs longer	**natalensis.**
	Light brown; filaments of palmate hairs shorter	**ardensis.**
6.	Median thoracic hairs overlapping occiput rudimentary	**maculipennis**
	Median thoracic hairs overlapping occiput well developed	7
7.	Internal anterior frontal hair branched	8
	Internal anterior frontal hair simple	9
8.	Palmate hair on second abdominal segment fully developed, the leaflets with a distinct shoulder; filaments of all palmate hairs about one-third as long as the whole leaflet.	**costalis.**
	Leaflets of palmate hair on second abdominal segment without shoulder; filaments of all other palmate hairs under one-quarter as long as the whole leaflet	**jacobi.**
9.	Hair at tip of antennae between the two spines split into two	**cinereus.**
	Hair at tip of antennae split into three	10
10.	Palmate hair on second abdominal segment well developed.	**pretoriensis.**
	Palmate hair on second abdominal segment rudimentary	**rufipes.**

Classification of the Culicinae

As has already been pointed out, Theobald places the mosquitoes in a separate family the Culicidae, which he divides it into ten subfamilies. The classification adopted by him and his followers has not, however, met with universal approval. Williston, one of the foremost systematic dipterologists, points out that nearly all the present-day culicidologists appear to have a limited knowledge of related Diptera, and as a result have disregarded broad zoological relationships and have erected subfamilies and genera on characters of minor value. He instances the subfamily Heptaphlebomyinae, which is erected on the single character of the presence of scales on the seventh longitudinal vien. He considers that scale characters are artificial, and that although they may be useful in separating the higher groups, they are of little use in splitting up genera; it is here that they are apt to be overrated. Williston's paper on the *Classification of the Culicidae*, and his remarks on the same subject in his volume on *North American Diptera*, should be read by all interested in the subject.

The following table, which gives the chief characters of the Culicidae, is taken from Volume IV of the *Culicidae of the World*.

Theobald's Table of the Subfamilies of the Culicidae.

A.	Scutellum simple, never trilobed. Proboscis straight; palpi long in male and female	**Anophelinae.**
AA.	Scutellum trilobed.	
a.	Proboscis strongly recurved; first submarginal cell very small	**Megarhininae.**
aa.	Proboscis straight; metanotum nude.	
1.	Wings with six long-scaled veins	2
	Wings with seven long-scaled veins	**Heptaphlebomyinae.**
2.	Antennae with second joint normal in length	3
	Second segment of antennae very long	**Deinoceratinae.**
3.	First submarginal cell as long or longer than second posterior cell	4
	First submarginal cell very small, smaller than second posterior cell	**Uranotaeninae.**
4.	Palpi of female shorter than proboscis, of the male longer.	**Culicinae.**
	Palpi short in male and female	**Aedinae.**
aaa.	Proboscis straight; metanotum with scales or chaetae	
5.	Palpi long in male short in female	**Trichoprosopninae.**
	Palpi short in male and female	**Dendromyinae.**
aaaa.	Proboscis elbowed	**Limatinae.**

Alcock suggests a simpler grouping of the Culicinae (sensu lato), which he divides into four sections as follows :—

Section 1. Megalorhinina (Megarhininae, Theobald). Mosquitoes in which the proboscis is very long and curved downwards, the apical part being much thinner than the basal. Palpi of the female either short or long. Wings narrow and somewhat elongated, the first 'fork cell' shorter than the second. Large, usually blue or green mosquitoes, non-biting, and with predaceous larvae.

Section 2. Culicina (Culicinae, Heptaphlebomyinae, Dinoceratinae, Aedinae and Uranotaeninae, Theobald). Mosquitoes in which the proboscis is of the usual type but not recurved; head clothed with different types of scales; palpi in the male long or short, many gradations existing between the two. Thorax round with a trilobed scutellum thickly covered with scales; metanotum without hairs or bristles. Wings, though rarely spotted, may be speckled or mottled.

Section 3. Metanotrichinia (Trichoprosopinae, Dendromyinae and Limatinae, Theobald). Mosquitoes in which the proboscis is of the usual type; the head, scutellum, and sometimes the thorax, are clothed with flat scales; palpi may be short in both sexes, or short in the female alone. Metanotum with a few bristles.

Section 4. Anophelina (Anophelinae, Theobald). Mosquitoes in which the proboscis is of the usual type; the head is clothed with upright forked scales, and never with flat scales; palpi as long as the proboscis in both sexes. Dorsal surface of thorax seldom densely clothed with scales. Scutellum simple, not lobed. Abdomen clothed with hairs or scales, the latter, if present, usually confined to the last segments, and then often inconspicuous. Wings as a rule spotted.

THE MEGALORHININA

This group of mosquitoes, according to Theobald, contains three genera *Megarhinus*, Robineau-Desvoidy, *Ankylorhynchus*, Lutz, and *Toxorhynchites*, Theobald; some of them are the most brilliantly coloured of all the mosquitoes; many of them have caudal tufts of hair-like scales on each side of the abdomen. Their large size, bright colours, and long bent proboscides are points which help in recognizing them. In *Megarhinus* and *Ankylorhynchus* the palpi are long in both sexes; in the former the last palpal segment in the female is rounded off, while in the latter it is round and pointed. In *Toxorhynchites* the palpi of the female are short, about one-third the length of the proboscis.

Theobald recognizes eleven species of *Megarhinus*, which are confined to North and South America and the West Indies; he states that the species described from India and Ceylon probably belong to *Toxorhynchites*. Peryassu and Bourroul have figured and described the larvae of some of the Brazilian species; they are all predaceous, and are found in water-buts and in holes in trees, where they live entirely on other mosquito larvae. The anal fin is wanting, but the terminal segment has four knob-like processes. The thorax is furnished with stout serrated spines and the abdomen has dense lateral tufts; the breathing syphon is rather short and ends in a valve with four flaps; the mandibles are very powerful. The whole larva is often blotched or streaked. The pupa has curved breathing trumpets, and two well-developed caudal fins. The eggs are elongated, pointed at one end and somewhat blunt at the other.

There are four species of *Ankylorhynchus* from South America, one of which has no caudal tufts at the end of the abdomen.

Theobald describes twenty-three species of *Toxorhynchites* from various parts of the world. *T. immisericors* is a common species in India, and breeds in holes in trees, in tanks, water-buts and tubs in which water is allowed to collect. The larvae are predaceous, though, in the case of some of the species, they do not feed on their own kind; the eggs are laid singly.

THE CULICINA

This section contains the well-known culicine mosquitoes, in which the scutellum is trilobed. The palps show extreme variations in length, some being as long or longer than the proboscis, others much shorter; they are, however, usually long in the male and short in the female, or moderately short in both sexes. Dyar and Knab have come to the conclusion that the length of the palps is a character of minor importance, and that too much stress should not be laid on it in splitting up the group. The character of the scale ornamentation is also very variable.

The Culicina (sensu lato) comprises the subfamilies Culicinae, Heptaphlebomyinae, Dinoceratinae, Aedinae, and Uranotaeninae of Theobald. Many of these groups contain a large number of genera, which cannot be described in detail here for want of space. The following table of the important genera is taken from Theobald's monograph, to which the reader is referred for further details.

Theobald's table of genera of the subfamily Culicinae (sensu restricto).

I. Eyes and scutellum normal.

- A. Legs ornamented with dense outstanding scales.
  - *a* Head clothed with spindle-shaped and broad curved scales.
    - β Hind legs only densely scaled . . . . . **Janthinosoma** (Aedes group).
    - ββ All the legs more or less densely scaled.
      - Wing scales rather thin . . . . . **Psorophora** (Aedes group).
      - Wing scales large inflated parti-coloured. Body and head with very long twisted scales . **Mucidus** (Aedes group).
- B. Legs normal, no irregular scales.
  - *a* Head clothed with flat and upright forked scales only.
    - β Scutellum with flat scales.
      - Small flat scales on the mesonotum before scutellum . . . . **Quasistegomyia** (Aedes group).
      - Flat scales as lateral patches also . . . **Kingia** (Aedes group).
    - No flat scales on mesonotum.
      - Male papli long, thin, nude and acuminate. Large . . . . **Desvoidya** (Aedes group).
      - Flat scales over the wing roots; proboscis very short and thick, bent twice; mid ungues of male equal . . . . **Brevirhynchus** (Aedes group).
      - Male palpi thin, acuminate or clavate, hairy. Small . . . . **Stegomyia** (Aedes group).

Ventral abdominal scale tufts . . . **Pseudocarrollia**
(Aedes group).

ββ Scutellum with narrow-curved scales.

Palpi of male acuminate . . . . . **Pseudoskusea**
(Aedes group).

Palpi of male clavate . . . . . . **Ludlowia**
(Aedes group).

Palpi of male clavate, marginal cell much contracted posteriorly. Shiny . . . . **Radioculex**
(Aedes group).

βββ Scutellum with flat scales at the base of the mid-lobe, narrow-curved at the border and a few on the lateral lobes. Legs very shiny . **Chaetocruiomyia**
(Aedes group).

aa Head clothed with mostly flat scales but also with small areas of narrow-curved scales and upright forked ones.

γ Scutellum with all flat scales.

δ Palpi of female very short.

Head with a median row of narrow-curved scales . . . . **Scutomyia**
(Aedes group).

Head with narrow-curved scales behind . **Aedimorphus**
(Aedes group).

Apex of abdomen very bristly; male palpi two-thirds the length of the proboscis. No hair tufts . . . . . . **Rachisoura**
(Aedes group).

Apex of abdomen very bristly; palpi of male smaller; wing scales straight linear and narrow spatulate . . . . . **Mimeteomyia**
(Aedes group).

δδ Palpi of female half length of proboscis.

Head with flat scales except for some spindle-shaped ones around the eyes . **Leicesteria**
(Aedes group).

As above, but a row of narrow-curved scales bordering eyes . . . . . **Duttonia**
(Aedes group).

γγ Scutellum with flat scales to mid lobe, narrow-curved ones to lateral lobes.

Head with flat scales, narrow-curved ones in median area . . . . . . **Macleaya**
(Aedes group).

Head with all flat scales except for a median basal area . . . . . . **Carrollia**
(Aedes group).

γγγ Scutellum with flat scales on each lobe separated by narrow-curved ones, an apical border of narrow-curved scales . . . . . **Popea**
(Aedes group).

γγγγ. Scutellum with flat and narrow-curved scales, none along apical border . . . . **Howardina**
(Aedes group).

γγγγγ. Scutellum with large spindle-shaped scales . **Huleocoeteomyia**
(Aedes group).

γγγγγγ. Scutellum with small flat scales on mid-lobe, narrow-curved ones on lateral lobes . . **Phagomyia**
(Aedes group).

Scutellum with small narrow flat scales on mid-lobe, narrow-curved ones over back, sides and border; lateral lobes with large narrow-curved scales. Wing scales *Taeniorhynchus*-like . . . . **Myxosquamus**
(Aedes group) ?

γγγγγγγ Scutellum with spindle-shaped scales on mid lobe, flat ones on lateral lobes . . . **Polyleptiomyia**
(Aedes group).

γγγγγγγγ Scutellum with narrow-curved scales all over.

δ Head with flat scales except for a median triangular narrow-curved scale area . **Pseudohowardinia**
(Aedes group).

δδ Flat scales spread around the eyes . . **Culiciomyia**
(Aedes group).

Flat scales loose; male palpi without hair tuft; shorter than proboscis . . **Eumelanomyia**
?

δδδ Head with only a double row of narrow-curved median scales . . . . **Neomacleaya**
(Aedes group).

δδδδ Head with all flat scales except along the nape **Danielsia**
Gualteria

Prothoracic lobes all with thick chaetae; fork cells small . . . . . **Hispidimyia**
?

δδδδδ Head with narrow-curved scales around the eyes . . . . **Lepidotomyia**
(Aedes group).

δδδδδδ Head with narrow-curved scales behind . **Gnophodromyia**
(Aedes group).

aaa Head clothed with mostly narrow-curved scales and upright forked ones, flat only at the sides as in *Culex*.

Scutellum with flat median and narrow-curved lateral scales . . . . **Protomacleaya**
(Aedes group).

Scutellum with all flat scales . . . . **Reedomyia**
(Aedes group).

Scutellum with mixed narrow-curved and small flat scales to mid lobe, long, flat and narrow-curved ones to lateral lobes . . . . **Pecomyia**
(Aedes group).

Scutellum with all flat scales, but a broad apical area to the mid lobe and some scattered ones on the lateral lobes . . . . . **Neopecomyia** (Aedes group).

Mid lobe of scutellum with broad curved scales, lateral lobes with flat and narrow-curved ones. **Stenoscutus** (Aedes group).

Scutellum with narrow-curved scales; first posterior cell uniform in breadth . . . **Bathosomyia** (Aedes group).

aaaa Head with loose irregular flat scales and narrow-curved ones behind.

Scutellum with flat median scales and narrow-curved lateral ones . . . . . . **Catageiomyia** (Aedes group).

aaaaa Head with broad flat spindle-shaped scales. Scutellum with small flat scales.

Vein scales of *Taeniorhynchus* type . . **Gilesia** (Aedes group).

Antennae densely hairy . . . . **Trichorhynchus** (Aedes group).

aaaaaa Head with broad narrow-curved scales; scutellum with flat scales; male palpi clavate, wings spotted. **Pseudotheobaldia** (Culex group).

Scutellum with broad spindle-shaped scales . **Maillotia** (Culex group).

aaaaaaa Head and scutellar scales narrow-curved only, except at the sides of the head where they are flat.

b Abdomen clothed with flat scales only.

I. Legs uniform, femora not enlarged at all.

Palpi of male clavate. Wings with lanceolate scales united into spots . . . . . **Theobaldia** (Culex group).

Wing scales scanty; wing membrane stained . **Pardomyia** (Culex group).

Wing scales pear-shaped and spatulate; fork cells short . . . . **Megaculex** (Culex group).

Wings with rather thick median scales and short broadish lateral ones. Fork-cells small; scales mottled.

Head with broad narrow-curved scales and forked ones.

Scutellum with narrow-curved scales . . . **Grabhamia** (Aedes group).

With mostly small flat scales on the scutellum, a few narrow-curved ones on posterior border of mid lobe . . . . **Pseudograbhamia** (Aedes group).

Head with irregular flat scales dotted all over giving a ragged appearance . . . **Acartomyia** (Aedes group).

Posterior cross-vein slopes prominently in basal direction, and median vein scales large and spatulate.	**Aporoculex** (Culex group).
Palpi of male acuminate. Wings ornamented with various coloured patches. Scales partly *Culex*-like, partly *Taeniorhynchus*-like	**Lutzia** (Culex group).
Wings with dense linear scales ; fork cells short.	**Culicada** (Aedes group).
Wings with broadish lateral vein scales, median large and spatulate. Front area of thorax silvery-grey scaled	**Leucomyia** (Culex group).
Fork cells short, but vein scales broader than in *Culex*	**Culicelsa** (Aedes group).
Wings with narrow linear or lanceolate scales. Fork cells long in the female. Costa not markedly spinose	**Culex**
Costa spinose ; male palpi bluntly acuminate.	**Microculex** (Culex group).
Wing scales broader than in *Culex* ; male palpi plumose	**Protoculex** (Aedes group).
Female palpi longer than in *Culex*, scales on basal and second antennal segments, male palpi enlarged apically dense hair tufts ; of three segments	**Banksinella** (Aedes group).
Male palpi of two segments	**Mimeteculex** (Aedes group).
Male antennae with special organs	**Lophoceratomyia** (Culex group).
Proboscis hairy in the middle	**Trichopronomyia** (Culex group).
Male palpi with an outstanding line of scales	**Pretinopalpus** (Culex group).
Wings with elongated broadish scales. Fork-cells long. Brown species. Proboscis banded.	**Taeniorhynchus** (Culex group).
Golden, yellow and purple species	**Chrysoconops** (Aedes group).
Wings with large broad and asymmetrical scales. Scutellar scales narrow-curved	**Mansonia** (Culex group).
Scutellar scales flat	**Mansonoides** (Culex group).
Wing scales large and fan-shaped	**Lepidoplatys** (Aedes group).
Wing scales heart-shaped	**Etorleptiomyia** (Culex group).

II. Femora and tibiae swollen apically and basally. Wing scales small, dense and broad at the apices of the veins. Small black gnats	**Melanoconion** (Culex group).
Wing scales longer and *Taeniorhynchus*-like	**Neomelanoconion** (Culex group).
Similar, but male palpi shorter than proboscis	**Protomelanoconion**
δδ Abdomen with large flat projecting lateral scales, with deeply dentate apices, in more or less dense tufts.	
Wing scales of *Culex* type	**Lasioconops** (Culex group).
δδδ Abdomen with scale ventral tufts.	
Wing scales pyriform, dense and mottled	**Finlaya** (Aedes group).
Scutellum nude except for two lines of scales.	
Head with small flat scales, with a median line of narrow-curved ones.	
Thorax mostly nude; scales on scutellum long and thin	**Bancroftia** (?)
Head with broad, short curved scales, those at sides broader and flatter but not spatuate; scutellar scales broadish.	**Pneumaculex** (Aedes group).
Near *Finlaya* but with mid-ventral abdominal scale tufts	**Orthopodomyia** (Culex group).
Near *Orthopodomyia* but male palpi longer, *Mansonia*-like scales on the wings and very long scales on the male antennae	**Newsteadina** (Aedes group).
II. Eyes very large, completely fused in middle line; scutellum with narrow scales	**Oculeomyia** (Culex group).
Scutellum with flat scales	**Molpemyia** (Aedes group).
III. Eyes small; scutellum with a large backwardly projecting process	**Rachionotomyia** (Aedes group).

The subfamily Heptaphlebomyinae contains the single genus *Heptaphlebomyia,* Theobald, with three species from West Africa and Madagascar. The subfamily Aedinae contains some nine or ten genera, a full description of which will be found in Theobald's monograph. The subfamily Deinoceratinae contains the two genera *Deinocerites* and *Dinomimites,* the larvae of which live in crab holes.

Edwards in a recent paper divides the Culicina (sensu lato) into two groups, as follows :—

Culex group. Eggs laid in masses ; the last segment of the abdomen of the female is broad and immoveable ; the claws of the female are never toothed.

Aedes group. Eggs laid singly ; last segment of the abdomen of the female narrow, usually completely retractile into the penultimate ; claws of the female, at least on the four anterior legs, nearly always toothed.

A few of the more important genera of the Culicina will now be considered in detail.

GENUS CULEX, L.

The head is clothed with narrow curved scales, upright forked scales and flat ones at the sides. The palpi are long in the male, short in the female ; the scutellum is covered with narrow curved scales.

Edwards would restrict this genus to those species in which the male palpi turn upwards and are longer than the proboscis, the fore and mid claws unequal, and the hind simple and equal. He regards the following generic names as synonyms ; *Heteroncyha*, Arrib. ; *Lasioconops*, Theo. ; *Melanoconion*, Theo. ; *Trichopronomyia*, Theo. ; *Neoculex*, Theo. ; *Pseudoheptaphlebomyia*, Ventr. ; *Mochlostyrax*, Dyar and Knab ; *Jamesia*, Christ. ; *Maillitia*, Theo. ; *Aporoculex*, Theo. ; *Leucomyia*, Theo. ; *Microculex*, Theo. ; *Oculeomyia*, Theo.

Culex fatigans, Wied. (Plate XXXVI, fig. 2). A medium-sized species, with a brown thorax marked with indistinct dark lines. Abdomen dark with pale creamy bands, and sometimes pale lateral spots. Legs dark brown, bases of femora, knee spots, and occasionally the apices of the tibiae, pale. Claws of fore and mid-legs of male unequal and uniserrated ; the hind claws simple and equal. It is widely distributed, and is mainly a house-frequenting species. It is believed to be the invertebrate host of *Filaria bancrofti*. In Madras, it is commonly infected with *Herpetomonas culicis*, Novy, MacNeal and Torrey.

GENUS TAENIORHYNCHUS, ARRIBALZAGA.

Palpi long in the male and short in the female ; head covered with narrow curved and upright forked scales. Wing scales broad to very broad, more or less bluntly pointed. The smaller claw on the fore and mid tarsi of the male not serrated, a marked characteristic of the genus.

All the species of the genus are of a yellowish colour and most are of medium size, though some are large insects.

Taeniorhynchus titillans, Walk. According to Edwards this species should be the type of Arribalzaga's genus, as it was evidently the species described by him in his elaborate description of *Taeniorhynchus*. This species, together with *pseudotitillians*, Theo., is said to act as the invertebrate host of *Filaria bancrofti*. *T. titillans* is a large river species common in South America; it has a brown thorax, dark palpi and proboscis, the latter sometimes with a trace of banding; abdomen dusky brown, sometimes with white scales on the sides; the legs are yellowish brown, femora and tibiae without bands, but tarsi with basal pale bands. *Pseudotitillans* is very like it, but is said to be smaller, and more reddish brown in colour, and has yellow apical bands on the abdomen. The eggs of most of the species of this genus are laid in long masses of two or more rows; the larva has a long- or short-pointed syphon.

GENUS MANSONOIDES, THEOBALD

Mosquitoes resembling those of the last genus, as regards the structure of the smaller claw of the fore and mid tarsi of the male, but with the palpi curved upwards as in Culex, and the last joint bent down at an angle to the penultimate one.

Mansonoides uniformis, Theobald. Allied to *T. titillans*, but the abdomen has apical lateral pale spots, and the legs are mottled and banded. This is a common species in South India, and is also found in many parts of the Oriental Region, as well as in the Ethiopian and Australian; it is found in swampy places, and in forests, where several observers have noted that it bites viciously; it is believed to be one of the invertebrate hosts of *Filaria bancrofti*.

GENUS STEGOMYIA, THEOBALD

The mosquitoes of this genus are mainly characterized by the white flat scales on the head and scutellum. Palpi long in the male and very short in the female. The thorax usually has white spots or bands; and the legs are black with white bands.

The genus *Stegomyia* belongs to the Aedes group, and is closely allied to *Ochlerotus*, Arrib., but differs from it by the thin male palpi. The external genitalia of the female are poorly developed, while those of the male are large and complex; the large and small claws of the male may be uniserrated or not.

The five common species of *Stegomyia* may be distinguished by the following Key:—

1.	Thorax with one or more white bands	2
	Thorax with one or more white spots	3
2.	Thorax with two median yellowish parallel lines and a curved white line on each side, the markings forming the so-called lyre pattern	**fasciata.**
	Thorax black with a median white line	**scutellaris.**
	Thorax with a median white line, and in addition, three parallel white bands on the pleura	**pseudoscutellaris.**
3.	Thorax black, with three or four white spots	**sugens.**
	Thorax black, with two white lines at the anterior end, and a white spot on each side at the base of the wing	**africana.**

Stegomyia fasciata, Fabr. (Plate XXXVI, fig. 1). Head with dark scales at sides, and median double band of white scales. Palpi black, thin and long, with two basal white bands in the male; in the female short, and either tipped with white or entirely white. Thorax dark brown to black, with whitish stripes simulating the shape of a lyre, the two median bands often yellowish; scutellum white. Abdomen covered with black scales, the bases of the segments with white scales forming transverse bands which extend round to the sides. Legs black, femora with silvery knee spots; metatarsi with broad white basal bands; the first tarsi of the fore and mid legs with a basal white band, the others black; first three tarsi of hind leg with broad white basal bands, the last tarsi pure white.

Stegomyia fasciata, commonly known as the 'Tiger' mosquito, is the invertebrate host of the parasite of Yellow Fever. When the female sucks the blood of a person suffering from this disease during the first three days of the fever, it becomes infected, and twelve days later it is infective. When once it becomes infective it remains so for the rest of its life, and is capable of transmitting the disease to a large number of people. It is not yet definitely known whether the parasite can infect the eggs, and thus the next generation. The virulent nature of the disease, and the great danger of its spreading from its endemic centres in Mexico and West Africa, have led to a most exhaustive study of the life history and habits of *Stegomyia fasciata*.

Bionomics of Stegomyia fasciata

The outstanding fact connected with the habits of this mosquito is that it is a true domestic insect, and is seldom, it ever, found more than 100 yards from inhabited houses; it prefers dark corners, and dark clothes, where it rests when not feeding. It frequently enters ships when they are moored

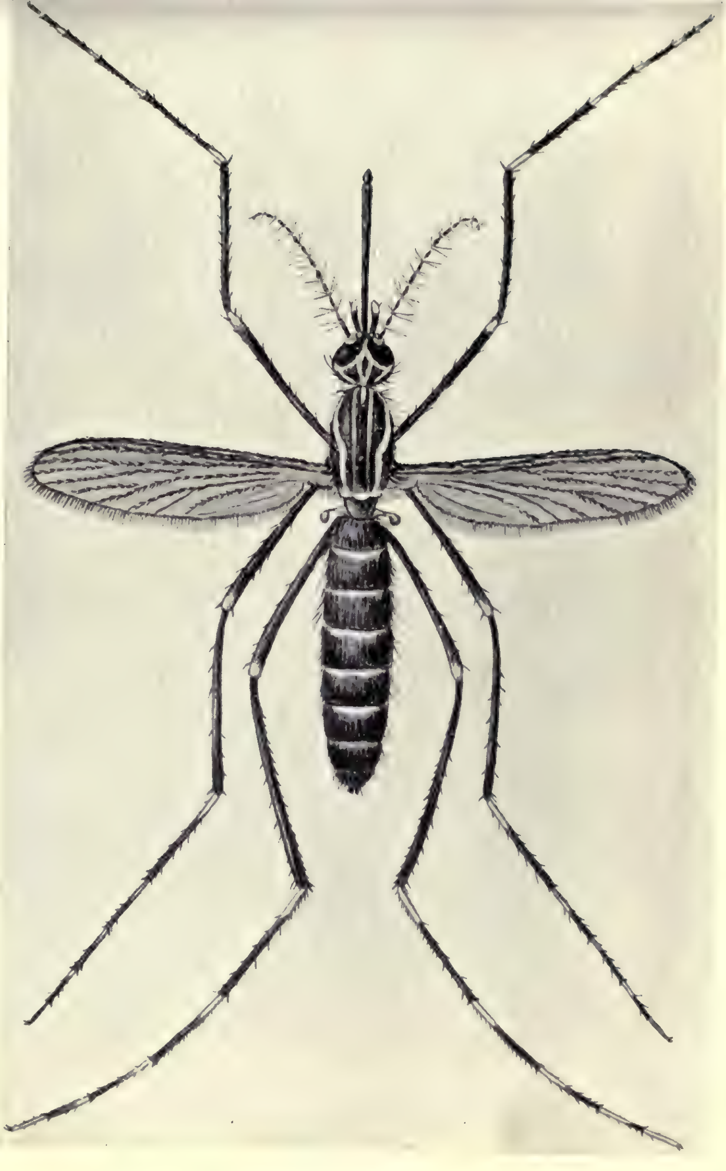

Fig. 1. Stegomyia fasciata, ♀. × 10.

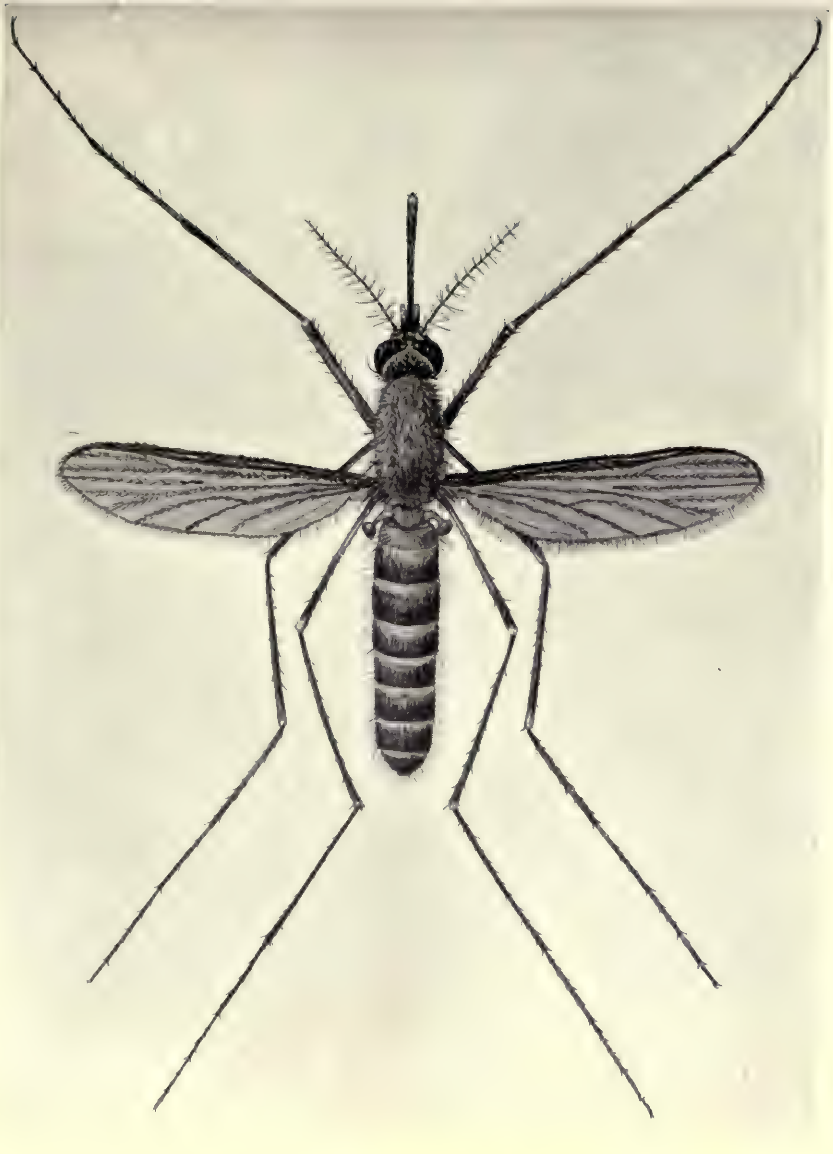

Fig. 2. Culex fatigans, ♀. × 10.

in harbours, and finds suitable hiding places in the holds and cabins. It bites during the day-time, especially in the afternoon, and occasionally after dark; Goeldi states that it sometimes bites at night like other mosquitoes. Copulation apparently takes place on the wing, and the males may often be seen accompanying the females; though they settle on the skin, they do not bite. It is generally believed that under natural conditions the female feeds only on vertebrate blood, but numerous experiments have been carried out to show that both sexes can be kept alive on sweet fluids for long periods. Goeldi, for instance, kept specimens alive for as long as 102 days, but no eggs were laid during this time; there can, therefore, be little doubt that *Stegomia fasciata* can live under natural conditions for a long time without blood; it is probable, however, that this food is necessary for the maturation of the eggs. The female can be kept alive for many months, and in nature can probably survive for at least six months.

Eggs are, as a rule, laid from five to sixteen days after the female takes her first feed of blood; Mitchell states that the female may feed three times before laying the first batch of eggs. There are usually three such batches, but there may be as many as nine; each egg is laid singly, and the total number laid at a time may vary from twelve to ninety or more. Goeldi thinks that, as a rule, the female lives about fourteen days after laying her last batch of eggs. He found that fertilized eggs may remain dormant for as long as 102 days, and might be laid even after this long period if the female took a feed of blood.

Stegomyia fasciata is widely distributed, and is found almost in every subtropical and tropical port, and from sea-level to 4000 feet or more above it.

Early Stages

The eggs, like those of most species of the genus *Stegomyia*, are black, elongated, and studded with what appear to be small whitish bodies, which produce the appearance of a frill; they hatch out in from three to four days, but may take as long as eight days. Theobald long ago discovered the important fact that the eggs were capable of resisting dessication for a considerable time. He was able to hatch out well-formed larvae from eggs which had been sent from Cuba in a dry test tube. In this connection Newstead has carried out more exact experiments. A batch of eggs which had been laid on moist filter paper at Manaos, South America, were first dried in the air, and later in a dessicator for twenty-four hours, and were then sent to England in a well-corked test tube. He gives the following data:—

September 9th to 11th	Eggs laid in Manaos.
October 26th	Eggs reached England. Placed in water at a temperature of 23° C (73·4° F).
October 27th	Twelve larvae hatched during the previous night, and one after 12 hours' immersion.
October 28th	Larvae began moulting.
October 30th	All larvae completed first moult.
November 4th	Larvae pupated.
November 7th	First imago, a male, hatched. It lived for six days.
November 8th	A male and female hatched.

In this experiment the eggs remained in a dormant condition for about forty-seven days. The incubation period after they were immersed in water lasted about twelve hours. The larval stage was completed in nine days, and the pupal stage lasted three days.

Francis has shown that the eggs of *S. fasciata* may remain viable as long as six and a half months when they are kept dry; they will not, however, hatch after two years. Peryassu found that after five months the eggs would not hatch. All these facts are of the utmost importance in connection with the spread of Yellow Fever.

The larva of this mosquito, like that of most of the genus, has a long body, and a not very well-defined thorax. The syphon tube is short and broad, and about one-quarter the length of the abdomen. The antenna has a single spine of medium length on the inner aspect, and a few small terminal hairs. The labial plate is described as having eleven lateral teeth, and a larger central one; its lower border is crenulated. The lateral combs on the eighth segment have about ten serrated spines. The spines on the syphon vary in number, and are not a reliable guide; they are, however, usually about eleven or twelve in number. The larvae have the power of remaining for long periods well below the surface of water. They are to be found in collections of water in buckets, pails, old tins, broken bottles, etc., in the vicinity of houses. They are commonly infected with a species of *Herpetomonas* and a spirochaete, both of which are found in the Malpighian tubes.

Stegomyia sugens, Wied. Thorax dark brown, marked with four, sometimes six, white spots; abdomen black; legs black with white bands; tarsi with basal white bands, the last tarsal joint of the hind leg pure white. This species is widely distributed in the Ethiopian region, and, like *fasciata*, is a domestic insect; it commonly breeds in buckets, roadside puddles, and especially in water which collects in holes in rocks; its larvae are often found in antiformicas.* It bites during the day and is often a most troublesome pest.

Stegomyia africana, Theo. Thorax black with two short intensely white bands, directed upwards on the anterior border, and a white spot at the base of each wing; pleura with silvery spots. Abdomen brown and unbanded with the exception of the last segment, which has two metallic spots. Legs black, hind tarsi with four white bands, the third broad and the fourth narrow. This species is common on the West Coast of Africa.

Stegomyia scutellaris, Walk. Thorax black, with a median white stripe. Abdomen black with white basal bands. Legs black, tarsi with basal white bands, and last tarsus of hind leg pure white. A common species in the Oriental Region, abounding in many of the Indian ports, where it breeds in earthen pots, wooden tubs, bamboo stumps, hollows in the trunks of trees, etc.

Stegomyia pseudoscutellaris, Theo. Closely allied to *scutellaris* but differs from it in having three white bands on the pleura, and those on the abdomen confined to the sides of the segments. It is said by Bahr to be the invertebrate host of *Filaria bancrofti*, and other species of filaria, in Fiji, where it is a domestic insect.

THE METANOTRICHINA

Theobald divides this group into three subfamilies, according to the characters of the palpi in the male and female. The metanotum is clothed with either scales or bristles, and the head and scutellum are covered with flat scales. All the species are found in jungles and forests, and it is very doubtful whether any of them are blood-suckers; at least they do not appear to bite man. Many are large brightly coloured insects, with irridescent wings. The majority are found in South America. The genus *Eratmapodites* contains a number of species from Tropical Africa. For further information the reader is referred to Theobald's monograph.

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* Tins filled with water in which the legs of tables are placed in order to prevent ants from crawling up.

THE ANOPHELINA

Mosquitoes for the most part with spotted wings, and assuming a characteristic tilted attitude when at rest, the proboscis and palpi being in the same plane as the thorax and abdomen. Palpi in both sexes, almost without exception, equal in length to the proboscis, and frequently spatulate at the tip in the male. Head covered with an abundance of upright forked scales, but never with flat scales; thorax and abdomen clothed with many hairs, occasionally with scales, and then usually on the last abdominal segments only; scutellum simple, never trilobed; metanotum bare or with a few hairs.

This group of mosquitoes contains the important species which are concerned in the transmission of the parasites of malaria, and it is therefore important for the worker to be able to identify them.

Theobald divides his subfamily Anophelinae into twenty-one genera. Alcock, however, considers that many of these cannot be separated as distinct genera, and he proposes grouping all under the single genus *Anopheles*, dividing it into seven subgenera as follows:—

Alcock's Synopsis of the subgenera of *Anopheles*.

A. The covering of the scutum consists mainly either of hairs or of narrow falculate scales. (In any doubtful case the palpi are slender, i. e. not shaggy with outstanding scales) 1

B. The covering of the scutum consists mainly of broadish elliptical, commonly recumbent scales 2

1. Abdomen either without scales or with some inconspicuous narrow scales on the genital lobes and terminal segment, or with a tuft of scales on the ventral surface of the penultimate segment 3

   Abdomen with an outstanding tuft of stiff and slender scales of extraordinary length on either side of every segment. **Christya.**

   Abdomen with broad and very conspicuous scales on several segments, some of the scales sometimes forming regular and outstanding tufts . . . . **Arribalzagla.**

3. Wings either not spotted at all or having a few dark spots formed merely by clumps of scales, or if 'variegated,' then there are not more than two distinctly formed colour-spots on the anterior edge. (In ambiguous cases, e.g. where a spot at the tip of the wing might be reckoned as anterior, then the palpi are shaggy) 4

   Wings usually much spotted in contrasted colours, their anterior edge barred or branded with numerous alternate dark and lights pots or streaks. (In any ambiguous case the palpi are not shaggy). Inconspicuous scales occasionally present on the terminal abdominal segment and genital lobes . . . . **Myzomyia.**

4. No scales on the abdomen (very rarely there may be a few scattered and inconspicuous scales on the genital lobes). **Anopheles.**
Abdominal scales present, usually as a small outstanding tuft on the ventral surface of the penultimate segment, rarely as a uniform covering to the terminal segment . **Myzorhynchus.**
2. The predominant scales of the head are of the 'upright forked' kind (cuneiform). . . . . **Nyssorhynchus.**
The predominant scales of the head are not 'upright forked'. **Chagasia.**

Alcock arranges the species of *Myzomyia* in two intergrading series as follows:—

a. The covering of the scutum consists mainly of hairs . . **Myzomyia.**
b. The covering of the scutum consists mainly of falculate scales. **Pyretophorus.**

The species of *Nyssorhynchus* he arranges in three distinct series as follows:—

a. Abdominal scales present on few of the distal segments . . **Nyssorhynchus**
b. Abdominal scales scattered on all the segments . . . **Neocellia.**
c. Abdominal scales fairly abundant on all the segments, and also in outstanding tufts which may be either lateral or ventral . . . . **Cellia.**

In the subgenus *Anopheles*, Meig., Alcock includes *Anopheles*, *Stethomyia* and *Cyclolepidopteron grabhami* of Theobald's monograph, and *Neostethopheles* and *Patagiamya* of James.

In the subgenus *Myzorhynchus*, Blanchard, are included *Myzorhynchus* and *Lophoscelomyia* of Theobald's monograph.

In the subgenus *Arribalzagia*, Theobald, are included *Arribalzagia*, *Kertezia*, and part of *Cyclolepidopteron* of Theobald's monograph.

In the subgenus *Myzomyia*, Blanchard, are included *Myzomyia*, *Feltinella*, *Neomyzomyia* and *Pyretophorus* of Theobald's monograph and *Nyssomyzomyia* of James.

In the subgenus *Nyssorhynchus*, Blanchard, are included *Nyssorhynchus*, *Neocellia* and *Cellia* of Theobald's monograph; *Calvertina* of Ludlow, and *Christophersia* of James.

In the subgenus *Chagasia*, Cruz, Alcock includes *Chagasia*, Cruz, and *Myzorhynchella*, Theobald.

In the descriptions which follow all the species will be referred to under the generic name *Anopheles* (sensu lato), the more restricted genera of Theobald being given in brackets so that the worker can refer to Theobald's classification of the genera of the subfamily Anophelinae, which is given below.

Theobald's Table of the Genera of the Anophelinae.

A. First submarginal cell large.
  I. Antennal segments without dense lateral scale tufts.

(*a*) Thorax and abdomen with hair-like curved scales.

α No flat scales on head, but upright forked ones.

β Basal lobe of male genitalia of one segment.

1. Wing scales rather large, lanceolate . . . **Anopheles.**
2. Wing scales mostly small, narrow or slightly lanceolate; wings prominently spotted along costa . . . **Myzomyia.**
3. Similar but fourth long vein very near base of third; outstanding scales on prothoracic lobes. **Neomyzomyia.**
4. Wings with patches of large inflated scales . **Cyclolepidopteron.**

ββ Basal lobe of male genitalia of two segments.

5. Prothoracic lobes with dense outstanding scales. **Feltinella.**

Median area of head with some flat scales; abdomen hairy; prothoracic lobes mammilated.

6. Wing scales lanceolate . . . **Stethomyia.**

(*b*) Thorax with distinct narrow-curved scales; abdomen hairy.

7. Wing scales small, lanceolate; head with normal forked scales . . . **Pyretophorus.**
8. Wing scales broad and lanceolate; head with broad scales, not closely appressed but not forked or fimbriated . . . **Myzorhynchella.**

(*c*) Thorax with hair-like curved scales, and some narrow curved ones in front; abdomen with apical lateral scale tufts and scaly venter; no ventral tuft.

9. Wing scales lanceolate . . . **Arribalzagia.**

(*d*) Thorax with hair-like curved scales; no lateral abdominal tufts; distinct apical ventral tuft. Palpi of female densely scaly.

10. Wings with dense large lanceolate scales . **Myzorhynchus.**

(*e*) Thorax with hair-like curved scales and some narrow-curved lateral ones; abdomen hairy with dense long hair-like lateral apical scaly tufts.

11. Wing scales short, lanceolate and dense; fork-cells rather short . . . **Christya.**

(*f*) Thorax with very long hair-like curved scales; abdomen pilose except last two segments, which are scaly; dense scale tufts on hind femora.

12. Wings with broadish, blunt lanceolate scales . **Lophoscelomyia.**

(*g*) Thorax and abdomen with scales.

13. Thoracic scales narrow-curved to spindle shaped; abdominal scales as lateral tufts and small dorsal patches of flat scales . . **Nyssorhynchus.**
14. Abdomen nearly completely scaly with long irregular scales and with lateral scale tufts . **Cellia.**
15. Similar to *Cellia* but no lateral scale tufts . **Neocellia.**
16. Abdomen completely scaled with large flat scales as in *Culex* . . . **Aldrichinella (Aldrichia).**
17. Thoracic scales hair-like except a few narrow-curved ones in front; abdominal scales long, broad and irregular . . . **Kerteszia.**

18. Thorax with narrow hair-like curved scales and some of them broad straight scales, others spatulate on the sides. Abdomen covered with fine hairs except the three last segments which are covered with scales. Tufts of scales on hind femora. Wing scales lanceolate . . . . **Manguinhosia.**

II. 19. Antennal segments with many densely scaly tufts **Chagasia.**

B. 20. Antennae with outstanding scales on the second segment, more oppressed ones on the first. At least one segment of abdomen with long flat more or less spatulate scales . . **Calvertina.**

21. First submarginal cell very small . . . **Bironella.**

To the above must be added the following new genera recently created by James:—

Abdomen with hairs but without scales of any kind. Thorax with hairs, and, as a rule, without scales of any kind, but in one or two species a few long and exceedingly narrow false scales may be present, chiefly on the anterior promontory. Thoracic lobes with hairs but without scales. Upright forked scales of the head very narrow in their whole length (linear or rod-shaped) . . . . **Neostethopheles**

Abdomen with hairs but without scales of any kind. Thorax with dorsum clothed with long, narrow, curved, sharp-pointed scales which form on the anterior promontory a thick bunch projecting over the neck. Prothoracic lobes with a conspicuous tuft of rather broad true scales projecting anteriorly. Upright forked cephalic scales of the usual broadly-expanding type . . . . **Patagiamyia.**

Abdomen with the first seven or six segments ornamented with hairs only. The eighth segment (sometimes also the seventh) and the genital process carry in addition a number of scales similar in character and arrangement to those of the group *Nyssorhynchus*. Thorax with the dorsum clothed with hairs and narrow-curved, sharp-pointed scales of various lengths and quite similar to those of the group *Myzomyia*. In addition there are on each side of the anterior third of the dorsum and beneath the angles of the anterior promontory some broader blunt-ended scales. Prothoracic lobes without a tuft of scales. Head with the usual type of upright forked scales . **Nyssomyzomyia.**

Abdomen with the dorsum of each segment thickly clothed with hairs and narrowly elliptical and blunt-ended scales which are not aggregated together to form tufts of any kind. The ventral surface of each segment is devoid of scales except that from the apices of six segments in the mid-line prominent tufts of long, blunt-ended, scales project directly downwards. These tufts resemble the single abdominal tuft present in the genus *Myzorhynchus*. Thorax clothed with rather narrow oblong and blunt-ended true scales. Prothoracic lobes with a prominent tuft of true scales. Head with the usual kind of upright forked scales . . . . . **Christophersia.**

INDIAN SPECIES OF ANOPHELES

The Indian species of *Anopheles* have been more thoroughly studied than those of any other country, and in James and Liston's Monograph, the second edition of which has recently appeared, the worker will find an accurate guide to the identification of the known species. Stephens and Christopher's pioneer work on the larvae of the Indian species is also worthy of note. The descriptions which follow are, in the main, taken from the works of the above authors. Many of the papers published in *Paludism* have also been consulted. The synoptic table prepared by Major Christophers, I.M.S., which is issued by the Central Malarial Bureau, Kasauli, will be found most useful, and is the easiest one to work with.

SYNOPTIC TABLE OF INDIAN ANOPHELES (FEMALES)

I. Wings unspotted.

a. Palpi unbanded. Tarsal joints unbanded.
  Anterior forked cell double the length of the posterior. Head scales very narrow linear . . . . . **aitkeni.**
  Anterior forked cell only slightly longer than the posterior. Head scales very narrow, linear, not broadly expanded as in most *Anopheles*, brown mosquito. **culiciformis.**
  Head scales expanded and forked as in most *Anopheles*. Hill species, large or moderate greyish, black mosquito. . . . . . . **barianensis.**
b. Palpi banded, tarsal joints banded . . . . . **immaculatus.**

II. Wings spotted.

A. Tip of hind legs white.

a. Legs not speckled. (Note 1).
  1. Two or three tarsal segments completely white. (Note 2).
    Wings more black than white. Costal spots white on dark ground. Spots small **fuliginosus.**
    Wings more light than black. Scales on abdominal segments except the first . . **fowleri.**
    Wings more light than black. Costal spots black on light ground. Spots very distinct. **pulcherrima.**
  2. One tarsal segment only completely white. (Note 2). Four broad white bands on palpi (including apex) . . . . . . **karwari.**
b. Legs speckled. (Note 1).
  1. Two or three tarsal segments completely white. (Note 2).

Palpi with four distinct bands. Beware of speckling imitating fourth band. (Note 1.) Speckling of legs generally indistinct . . . . **pulcherrima.**

Palpi with three bands including apex. Beware of speckling imitating fourth band.

Palpi prominently speckled. (Note 3.) Palpi with two broad apical bands, one narrow basal. Three hind tarsal segments completely white. Leg speckling pronounced. **maculipalpis.**

Palpi not speckled.

Three hind tarsal segments completely white. One broad apical palpal band, two narrow. Leg speckling not very pronounced . . . . **jamesi.**

Two hind tarsal segments completely white. Broad white band above this. Palpi with two broad apical, one narrow basal band **theobaldi.**

2. One tarsal segment or less, completely white. (Note 2.)

There may be white tarsal banding as well.

Palpi with four well marked white bands (beware of speckling imitating fourth band).

Half last tarsal segment white. Black ventral scale tufts visible to naked eye. Three spots on sixth longitudinal vein. . . **halli.**

Extreme tip of last tarsal segment only white. Five or six spots on sixth longitudinal vein.

Tibio-tarsal joints of hind legs broadly banded white , , , , , **elegans.**

Tibio-tarsal joints not broadly banded white . **punctulata.**

Palpi with three bands (including apex)

Tip of palpi white.

Many scales on abdomen . . . . . **willmori.**

Scales only on last few segments . . . **maculatus.**

Tip of palpi black . . . . . . **indica.**

B. Tip of hind legs not white.

a. Legs not speckled.

1. Hind tarsi banded (joints light).

Palpi unbanded.

Wings more black than white. White spots small . **barbirostris.**

Wings more light than black. Spots large and distinct. Hill species . . . . **gigas.**

Palpi with distinct bands.

Tip of palpi black . . . . **turkhudi.**

Tip of palpi white.

Front tarsal joints broadly banded. Brown mosquito. **rossii.**

Front tarsal joints not broadly banded. Numerous fringe spots. Dark species. Third long vein light. **jeyporiensis.**

A single fringe spot. Lighter species. Third long vein dark . . . . **culicifacies.**

Palpi with narrow bands.

Wings more black than white. White spots small . **nigerrimus.**

Wings more light than black. Spots large and distinct. Hill species . . . . **simlensis.**

2. Hind tarsal joints not banded.

Palpi unbanded, broad white band on femur. Hill species . . . . **lindesayi.**

Palpi banded.

A single fringe spot. Third long vein dark . . **culicifacies.**

Numerous frings spots. Third long vein light.

Tip of palpi white.

Narrow almost hair-like scales on thorax. Stem of second long vein mostly dark . . . . . **listoni.**

Broad scales on thorax. Stem of second long vein mostly light . . . . **nursei.**

Tip of palpi black.

Narrow almost hair-like scales on thorax. Stem of second long vein mostly dark . . . . . **turkhudi.**

Broad scales on thorax. Stem of second long vein mostly light . . . . **nigrifasciatus.**

b. Legs speckled (Femora and tibiae spotted).

1. Palpi with four well marked white bands (Beware of speckling imitating fourth palpal band).

Tibio-tarsal joint of hind leg forms broad white conspicuous band . . . . **elegans.**

Tibio-tarsal joint of hind leg without broad white band. **punctulata.**

2. Palpi with three well marked bands. Beware of speckling imitating fourth band.

Palpi with two broad apical and narrow basal bands. Palpi speckled. Scales on nearly all abdominal segments . . . . **stephensi.**

Palpi with one broad apical and two narrow bands palpi not speckled. Scales confined to last segment or so . . . . **ludlowi.**

In using the above key Christophers draws attention to the following points:—

Note 1.—Speckling on the legs means spotting or banding of the femur and tibia, (not banding of the tarsal joints.) Speckling is if present distinct. A faint mottling is not considered as speckling.

Note 2.—Tarsal segments completely white are counted from the tip, stopping at the first dark band. If the tip is white, for from 1/12″ to ⅛″, two or three segments are pure white. If the amount of terminal white is very small, one or less segments only are white.

Note 3.—Speckling on the palpi refers to white spots on the dorsal surface, usually between the middle and basal palpal band.

Species entered in more than one place may show sometimes one appearance and sometimes another (e. g. tarsal banding in *culicifacies*) or an appearance may be overlooked (e. g., the minute point of white on the extreme tip of the hind tarsi of *punctulata*.) In either case the table will work out correctly.

Anopheles (*Nyssomyzomyia*) *rossii*, Giles. (Plate XXXVII, fig. 1.) Palpi brown with three white bands, the apical being the broadest. Thorax fawn coloured. Abdomen brown. Legs brown, the distal ends of the femora, tibiae, and all the tarsal segments except the last, with

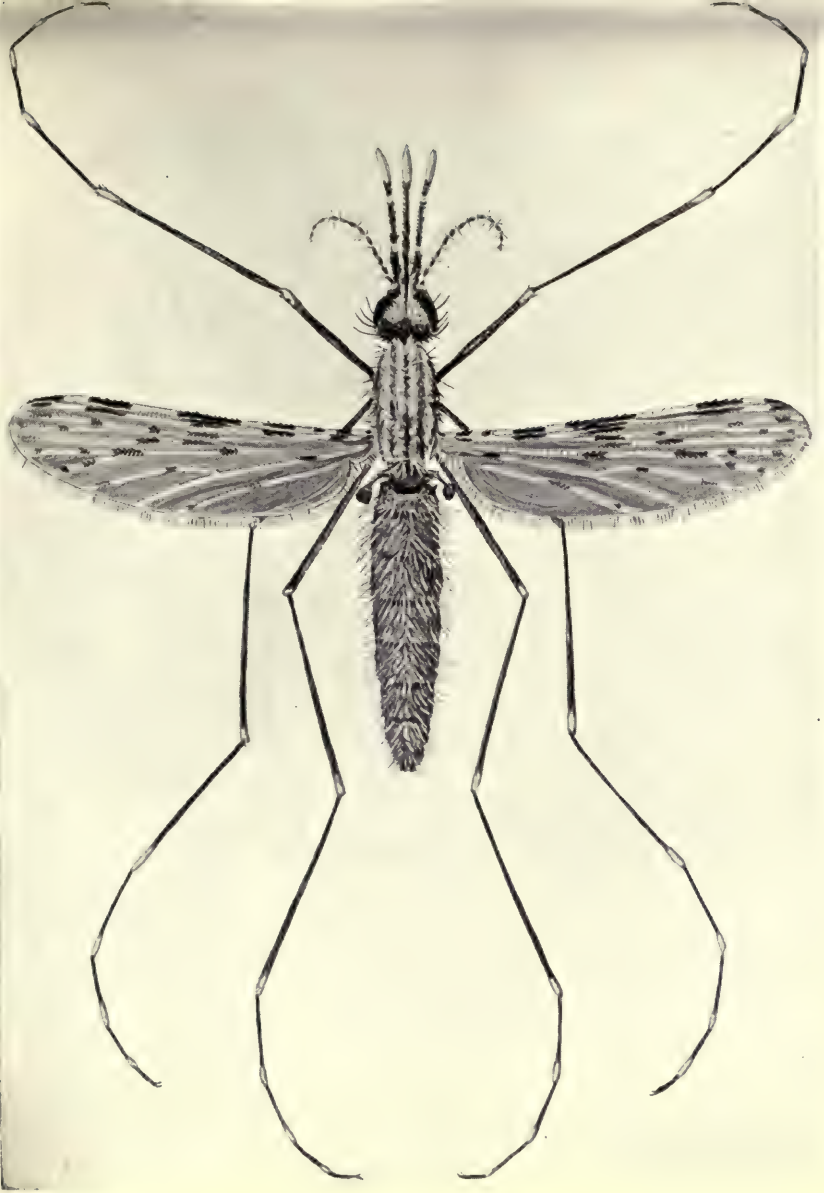

Fig. 1. Anopheles rossii, ♀ × 12.

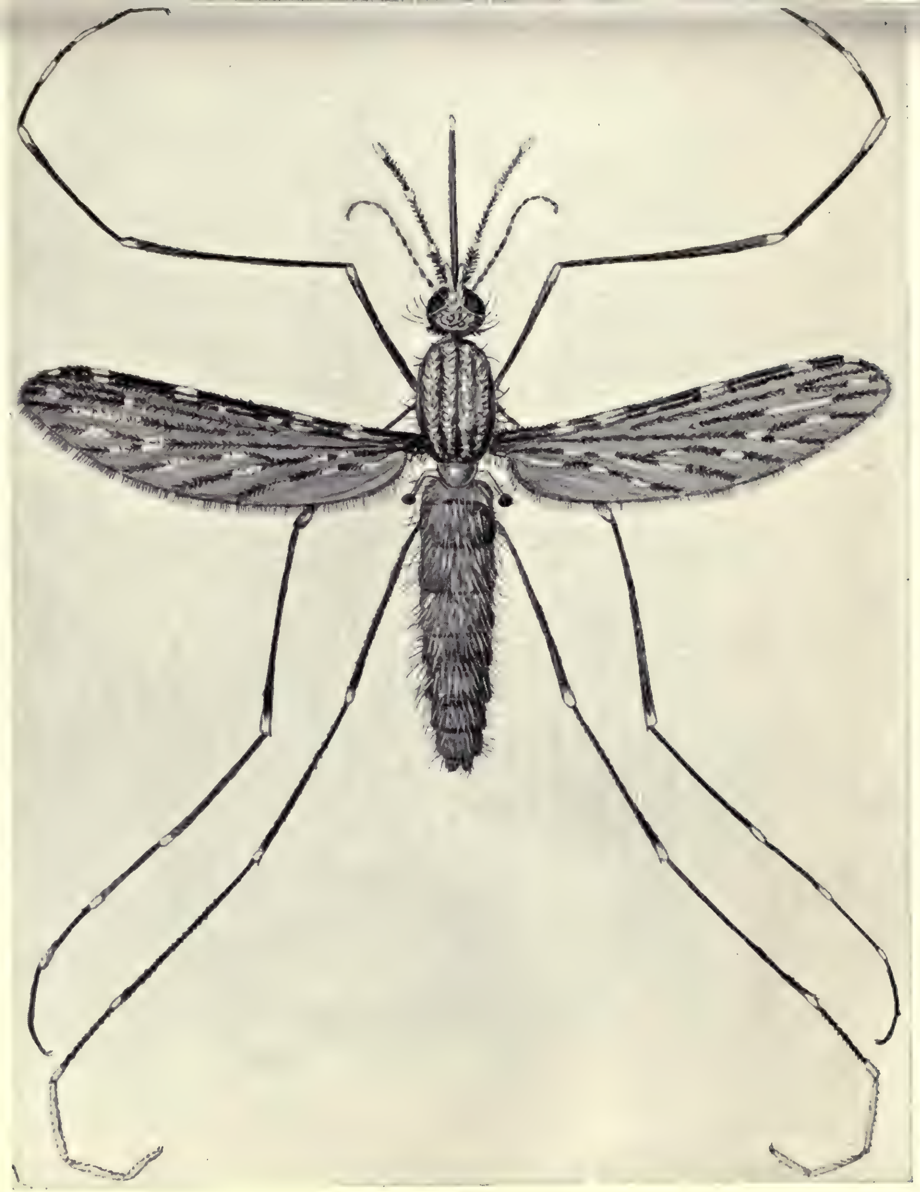

Fig. 2. Anopheles fuliginosus, ♀ × 14.

narrow white bands. Costa of wing with six or seven black spots, the three first small and often joined. Upper surface of egg with a broad frill round it; floats arising from the fringe and touching its margin. Larva with frontal hairs simple and unbranched; palmate hairs from second to seventh abdominal segments; leaflet very long and as a rule with a single serration.

This species is distributed almost throughout India, and has been found at a height of 5,000 feet; it is also common in the Straits Settlements, Sumatra, Java, and the Philippine Islands. It is essentially a domestic insect, and breeds as a rule in shallow pools, washings from houses, in paddy fields and even in the backwaters along the Madras Coast; it is common throughout the year. As far as is known at present it plays no part in the transmission of malaria in nature, though it can be infected in the laboratory. In a recent paper Bentley shows that *rossii* is refractory to malarial infection in nature. Vögel, working in Java, suggests that only adults which were bred from larvae living in salt water become infected; this statement is, however, disproved by the experiments of Stephens and Christophers, for these observers were able to infect adults which were bred out of larvae living in fresh water.

Christophers records a variety of *rossii* from the Andaman Islands which has a broader white apical band on the palps; it is probably identical with *Anopheles indefinita*, Ludlow. It breeds in small and temporary collections of water among houses, and appears to be restricted to the vicinity of human dwellings.

Anopheles (*Nyssomyzomyia*) *ludlowi*, Theobald. Palpi with three white bands as in *rossii*, but the apical band is narrower. Thorax dark brown with light areas. Abdomen clothed with golden brown hairs. Legs speckled and with white bands at all the tarsal joints. Costa with six or seven black spots like those of *rossii*; the basal spots are sometimes longer. Its egg, according to Christophers, has a narrow frill and in general appearance simulates that of *fuliginosus*.

Ludlowi is found in Bengal, Burma, the Andaman Islands and the Philippine Islands. In the Andamans, where Christophers has demonstrated it to be a carrier of the parasites of malaria, it is never found more than a quarter of a mile from salt water. The larvae were found in brackish water near embankments, and in one instance Christophers notes the water contained about four per cent of salt.

Anopheles (*Nyssomyzomyia*) *punctulata*, James and Liston. Palpi with four white bands and speckled on basal half; the apical band is narrow, the next two broad, and the fourth narrow. Thorax clothed with hairs and narrow scales. Abdomen also covered with hairs, and with a few scales on the last segment. Legs speckled, first tarsi of fore and mid legs with a distal white band. Costa with seven dark spots, the smallest at the base; apex of wing with white scales. Egg, larva and pupa unknown. This species has been found in the Central Provinces, at Karwar, at Parel in the Bombay Presidency, in Delhi and in the Andaman Islands. Its habits are unknown. It is possibly identical with *Anopheles* (*Cellia*) *punctulata*, Dönitz.

Anopheles (*Neomyzomyia*) *elegans*, James. Palpi with four white bands, the apical band the broadest. Thorax brown to grey, with dark longitudinal lines and eye spots. Abdomen brown with dark hairs. Legs brown with white speckling, a broad white band at the junction of the tibiae and metatarsi of hind legs. Costa with four large black spots, and sometimes two or three small basal ones. Egg unknown. Larva with simple median and external frontal hairs; palmate hairs only present on the abdominal segments, leaflet with short stumpy filament. This species is found in Karwar, and in the Andaman Islands, where, according to Christophers, it breeds in rocky mountain streams in the forest.

Anopheles (*Neostethopheles*) *aitkeni*, James (in Theobald). Palpi dark without any bands. Thorax dark brown. Abdomen black with long hairs. Legs brown, without any bands or spots. Wing unspotted; first submarginal cell almost double the length of the second posterior cell. Egg unknown. Larva with median frontal hair branched into fork-like prongs; external hairs simple and short. Palmate hairs on second to seventh abdominal segments; leaflets long with short spear-like filaments. This species occurs at Karwar, and on the Frontier of Goa, in the Bengal Duars, and in the Andaman Islands. Its habits are unknown.

Anopheles (*Neostethopheles*) *culiciformis*, James and Liston. Palpi brown, without bands. Thorax clothed for the most part with brown hairs. Abdomen brown, covered with golden hairs. Legs long, unbanded. Costa without any spots. Egg unknown. Larva with simple and unbranched frontal hairs, the external ones short, the median long and close together. A long hair with a swollen end and a tuft of fine hairs just behind each antenna. Palmate hairs present on thorax and all abdominal segments; leaflet long and pointed, like a thorn, and without any definite filament. A long unbranched hair on the side of the third abdominal segment. This species is found at Karwar in the Bombay Presidency. When resting on the wall its attitude is like that of *Culex*. Its habits are unknown.

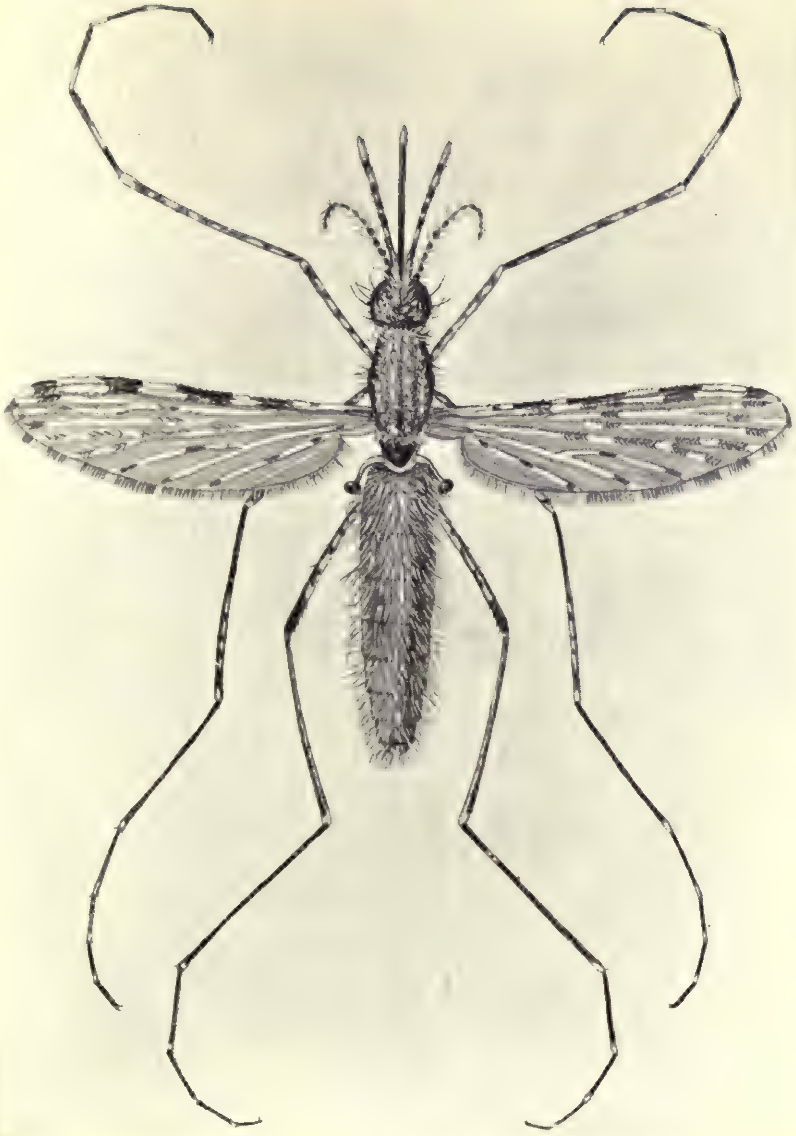

Fig. 1. Anopheles stephensi, ♀. × 12.

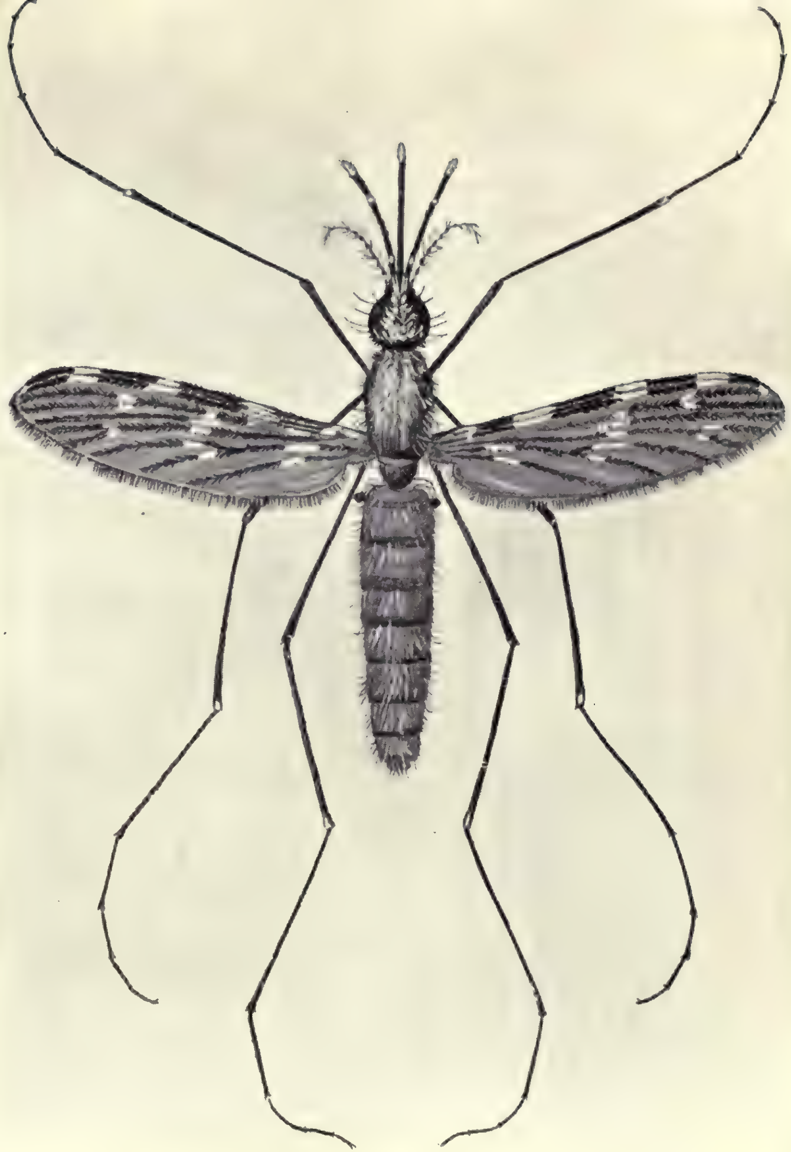

Fig. 2. Anopheles culicifacies, ♀. × 12.

Anopheles (*Patagiamyia*) *lindesayi*, Giles. Palpi black, without any bands. Thorax black with a large dorsal rectangular whitish area. Abdomen black with long hairs. Legs black with a long white band at the middle third of the hind femora. Costa almost entirely dark, with a characteristic yellow spot at the apex. Egg unknown. Larva with simple and unbranched frontal hairs; antenna with a small branched hair. Palmate hairs absent on thorax, well developed on second to seventh abdominal segments; leaflet long with a moderately pointed filament. This is chiefly a hill species and is found in Simla, Murree, and other hill stations in India.

Anopheles (*Patagiamyia*) *gigas*, Giles. According to Giles, James and Liston, the palpi are brown and unbanded. Thorax with a dark rim of chocolate colour and a large rectangular area on dorsum. Abdomen broad with golden hairs. Legs light brown, with pale bands at the tarsal joints. Costa with four black spots, two small basal and two long median and apical ones. Egg and larva unknown. This species was first recorded from Coonoor, Nilghiri Hills, South India; it has been taken by one of the authors at Kodaikanal, Pulney Hills, South India, while feeding on a horse during the day. It is a wild mosquito, and was never seen in a house in Kodaikanal.

Anopheles (*Patagiamyia*) *simlensis*, James. Closely allied to *gigas*, and only differs in having banded palpi. According to James and Liston the larva of *simlensis* has simple and unbranched frontal hairs; a small branched hair on the antenna; palmate hairs are present on the third to the seventh abdominal segments, and the leaflet is short with a stumpy filament.

Anopheles (*Myzomyia*) *culicifacies*, Giles. (Plate XXXVIII, fig. 1.) Palpi with three small yellow bands of equal size, the tip forming one of the bands. Thorax yellowish brown with a dark median line. Abdomen brown with yellowish brown hairs. Legs dark brown, with small yellowish spots at the joints. Costa with five black spots, the basal spot being the smallest. Egg (Plate XXXIV, fig. 10) with a narrow rim on the upper surface, the floats not extending up to it. Larva with simple unbranched frontal hairs; palmate hairs present on the thorax and all the abdominal segments; each leaflet serrated and with a moderately fine filament. This species is widely distributed in India, and is found in the Punjab throughout the hot weather, but to a much less extent in the colder months; it is common in many parts of Bengal, the United Provinces, Bombay, the Central Provinces, Berars, Burma and the Madras Presidency, especially in Ennur and the Jeypore Agency tracts. The larvae are found in pools of rain water, paddy fields, borrow pits, pools in dry river beds, and in fact almost any collection of natural or artificial water; it also breeds in wells.

It is one of the most important natural carriers of the parasites of malaria. The mature insects are somewhat difficult to detect, and when in dark corners may escape observation, their *culex*-like attitude being very deceptive. A variety ***punjabensis*** is recorded by James and Liston, and is said to differ from the type *culicifacies* by the complete absence of the fourth dark area on the costa and first long vein.

Anopheles (*Myzomyia*) *listoni*,* Liston. Palpi with three white bands, one situated at the tip. Thorax yellowish brown, with a median and two indistinct lateral lines. Abdomen very dark, almost black, with some yellowish white hairs. Legs broad and marked like those of *culicifacies*, except that the light patch at the apex of tibia is nearly always absent. Costa with four black spots, basal spot as a rule not divided into two as in *culicifacies*. Egg with the upper surface narrow, divided into two parts, each with a narrow frill; floats long with about twenty crinkles, and not encroaching on the upper surface. Larva with simple and unbranched frontal hairs; palmate hairs on thorax and all abdominal segments; leaflet moderately long and serrated, and with filament similar to that of *culicifacies*. This species is common in the Berars, Central Provinces, Bengal Duars, Jeypore Agency, Goa, Bombay, Hyderabad (Deccan,) and the North Canara District. Theobald states that it occurs in Ceylon and Perak.

It breeds in running streams, and is probably a natural carrier of the parasites of malaria wherever it occurs. It is often difficult to distinguish it from *culicifacies*; James and Liston in their monograph state that the length of the first submarginal and first posterior cells are the best means of separating the two species. If the first submarginal cell is more than half as long as the second posterior, the specimen is *listoni*, if the reverse it is *culicifacies*.

Anopheles (*Myzomyia*) *leptomeres*, Theobald, is, according to James and Liston, a variety of *listoni*.

Anopheles (sensu restricto) *barianensis*, James. Palpi black without any bands. Thorax dark brown. Abdomen almost black, dorsal surface of each segment with greyish white areas. Legs broad, coxae and trochanters white, otherwise unbanded. Costa without spots.

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* It appears that when describing this species under the name *listoni*, Major Liston believed he was dealing with *listoni*, Giles, which is now known to be a distinct species. Major Liston's description, therefore, holds priority.

Early stages unknown. It is found at Barian in the Murree Hills in the Punjab. Its habits are unknown.

Anopheles (sensu restricto) *immaculatus*, Theobald and James. Palpi with three whitish bands, basal ones narrow, apical band broad. Thorax ash grey with a dark median line. Abdomen brown with golden hairs. Legs brown, apices of tarsal joints with bands, best seen in the hind tarsi. Costa without spots. Early stages and habits unknown, and the male has not been recorded. It was found at Ennur near Madras, by Stephens.

Anopheles (sensu restricto) *turkhudi*, Liston. Palpi with three white bands, apices black. Thorax brown with a median light rectangular area. Abdomen olive green, with golden hairs; legs brown with yellow patches at the apices of the femora and tibiae. Costa with six black spots, two situated near the base. Egg bullet-shaped, one end more rounded than the other; the upper surface with a rudimentary rim near the rounded end; floats entirely wanting. Larva with simple and unbranched frontal hairs, and a posterior one on each side, unbranched and projecting over the oral cavity between the frontal hairs; palmate hairs only present on the fourth to the seventh segments; leaflet long, spear-shaped, serrated, and without any free filament. The larva rests at the surface of the water in a *culex*-like attitude. This species is common in the Berars, Central Provinces, Kashmere, and in the Punjab. It breeds chiefly in clear pools, especially in pools in dry river beds, during the rains. It is not known to be a natural carrier of the parasites of malaria, but it can be infected in the laboratory.

Anopheles (*Pyretophorus*) *jeyporiensis*, James. Palpi with three white bands; the apical one, which includes the tip, is broader than the others. Thorax with somewhat dark lines. Abdomen dark brown with golden hairs. Legs dark, with very small clear white bands at all the joints. Costa with six black spots, the basal one small. Egg unknown. Larva with frontal hairs thickly branched, and a posterior one, also branched, between them; palmate hairs present on thorax and abdominal segments, not unlike those of *listoni* but broader, with the filament much shorter. It is found in the Jeypore Agency in the Madras Presidency, also in the Central Provinces and in several parts of South India. The larvae are usually found in streams, and in irrigation channels in rice fields.

Anopheles (*Pyretophorus*) *nigrifaciatus*, Theobald. Palpi with three white bands, the apices black. Thorax ash grey in the middle, and brown at the sides. Abdomen brown with golden hairs. Legs brown, unbanded. Costa with four large black spots and two smaller ones.

Egg and larva unknown. The species is fairly common in Quetta at certain times of the year. Mrs. Davys says that it breeds in open pools, and irrigation channels.

Anopheles (*Pyretophorus*) *nursei*, Theobald. Closely allied to *nigrifasciatus*; palpi with a well-marked apical white band. According to Mrs. Davys it is one of the commonest anophelines in Quetta, and breeds in the same kind of places as *nigrifasciatus*; the larvae are able to remain as long as eight minutes below the surface.

Anopheles (*Nyssorhynchus*) *maculatus*, Theobald. Palpi with three white bands, the apical one including the tip, and only separated from the next by a narrow dark band. Thorax brown with lighter sides. Abdomen dark brown. Legs brown and speckled; the last tarsal segment of the hind leg is entirely white. Costa with four long black spots, and three smaller basal ones. Egg with frill interrupted by the floats, which touch the upper margin; floats short, about one-third the length of egg. Larva with simple and unbranched frontal hairs; palmate hairs present on second to seventh abdominal segments; leaflet moderately long, filament very short. This species is common in the Bengal Duars.

Anopheles (*Nyssorhynchus*) *fuliginosus*, Giles. (Plate XXXVII, fig. 2.) Palpi black with three white bands, the basal one narrow, the next broader, and the apical one, which includes the tip, broad. Thorax dark brown. Abdomen dark, almost black. Legs black, narrow, with distinct bands at the fore and mid tarsal joints; last three tarsi of hind leg pure white. Costa with six long black spots separated by small white spots. Egg (Plate XXXIV, fig. 8) with rather broad upper surface and well-marked frill, which is encroached on by the floats. Larva with frontal hairs with few branches, the external with more than the internal. Palmate hairs only present on the abdominal segments; leaflet moderately long, serrated and with a long spine.

This species is widely distributed, and is common in Calcutta and other parts of Bengal, in many parts of the Punjab, in Bombay, Goa, and the Central Provinces; it is also common in many places in South India, including Madras City. It breeds in pools, ponds and tanks with vegetation at the sides, and is a natural carrier of the parasites of malaria.

Adie has noted a distinct but unnamed variety, in which the palpi have four narrow white bands, and the last two and a half or two and three-quarters of the hind tarsal segments are white. It is found at Ferozpore and Amritsar in the Punjab, but only at certain seasons.

Another variety *nagpori*, James and Liston, is found in the Central Provinces and in the Punjab. The palpi are black tipped, and two and one-third tarsal segments of the hind leg are white.

Anopheles (*Nyssorhynchus*) *jamesi*, Theobald. Palpi black with three white bands, the apical band including the tip, and broader than the others. Thorax black, clothed with short white scales. Abdomen black with whitish scales. Legs light brown and speckled, four tarsal bands on fore and mid legs; in hind legs last three tarsal segments pure white. Costa with six black spots, the two basal ones being small. Larva with branched frontal hairs. Palmate hairs on the first to the seventh abdominal segments, rudimentary ones on the thorax. This species is common in Bengal, Central Provinces, and in parts of South India; it is occasionally seen in Madras City.

Anopheles (*Nyssorhynchus*) *maculipalpis*, James and Liston. Palpi black, with three white bands, and specks of white between them. Thorax black, clothed with white scales. Abdomen dark with a white sheen. Legs black, spotted all over, the last three and a part of the second hind tarsi pure white. Costa with four black spots, and two smaller ones near the base. Egg with a narrow rim, floats arising from it, but not altering its contour. Larva with frontal hairs thickly branched. Palmate hairs or the thorax as well as the abdominal segments; leaflets moderately long with a medium-sized pointed filament. This species is found in the Central Provinces, Bombay Presidency, South India, and at Drosh in Chitral.

Anopheles (*Nyssorhynchus*) *theobaldi*, Giles. Palpi with three white bands, the apical one including the tip, the basal band very narrow. Thorax black, with cream coloured scales and white hairs. Abdomen black with white hairs. Legs dark and much speckled, last two segments of hind tarsi pure white. Costa with six black spots, the basal one small. Larva with slightly branched frontal hairs. Palmate hairs rudimentary on the thorax but present on all abdominal segments; leaflet moderately long, filament very short and blunt. This species is found in the Berars, Central Provinces, Jeypore State, and Karwar in the Bombay Presidency. It breeds in streams.

Anopheles (*Nyssorhynchus*) *karwari*, James. Palpi with four white bands, the apical one including the tip. Thorax dark, almost black, with snowy white scales. Abdomen black with golden scales. Legs dark without any speckling, except on the fourth and fifth tarsal segments of the fore and mid legs; all the others have distal white bands; the tibiae and all the tarsal segments of the hind legs have white bands at their distal ends, the third and fourth segments also at their proximal ends; the last segment is entirely white. Costa with one large, three medium sized, and two basal small black spots. Larva with frontal hairs simple and unbranched. Palmate hairs absent on the thorax. This species is found in Karwar and Goa and most probably in other parts of the Bombay Presidency; it is also common at certain seasons in the Bengal Duars; Leicester records it from Malay.

Anopheles (*Neocellia*) *indica*, Theobald. Palpi dark, with three white bands, the apices dark. Thorax with a frosty sheen. Abdomen brown to black, legs with femora, tibiae, and all the first tarsal segments spotted; second tarsal segment of hind leg with a broad white band, the third and fourth with bands at both ends, and the fifth entirely white. Costa with six black spots, the two basal ones small. This species is found at Dehra Dun and other places at the foot of the Himalayas.

Anopheles (*Neocellia*) *willmori*, James. Palpi black, with three white bands, the apical one including the tip. Thorax greyish brown. Abdomen dark, covered with white scales and hairs. Legs dark brown, extensively speckled with white spots; the distal end of the second hind tarsal segment has a broad white band continuous with a similar band on the upper end of the third segment, the third and fourth segments have broad apical and basal bands, and the last segment is entirely white. Costa with four large and three small basal black spots. The egg is of the *listoni* type, the upper surface being narrow. Larva with simple and unbranched frontal hairs, and a well developed posterior hair. Palmate hairs well marked from the third to the seventh segments, rudimentary on the second; the leaflet is moderately long, serrated, and has a short filament. This important species is widely distributed in the Punjab and Kashmir; it is found at Pathankot, and in the Kangra valley, where Mrs. Adie has found it infected with sporozoits; it is common at Murree, Almorah, and in parts of Chitral. It breeds in streams and clear pools.

A variety *maculosa*, James and Liston, is said to be abundant at the foot of the Himalayas; it differs from the type in having several white patches between the two proximal palpal bands in addition to the usual markings.

Anopheles (*Neocellia*) *stephensi*, Liston. (Plate XXXVIII, fig. 2.) Palpi with three white bands and some intermediate white patches; the apical band is broad and includes the tip. Thorax light brown, sometimes much darker. Abdomen dark brown. Legs brown, speckled and not conspicuously banded, the last tarsal segment of the hind leg is entirely dark. Costa with six black spots, the two basal ones small. Egg (Plate XXXIV, fig. 2) with a broad upper surface, the floats arising from the rim. Larva with simple and unbranched frontal hairs. Palmate hairs only on the abdominal segments; leaflet long and pointed, very similar to that of *rossii*, but rather shorter. This species occurs almost all over the plains of India; it has been recorded from the Punjab, Bengal, Bombay, Central Provinces, the Berars, Sind, Assam, and South India. It is an important natural carrier of the parasites of malaria. Bentley, who has made a careful study of its habits in Bombay, notes that it is a domestic species, breeding in wells and cisterns, in collections of fresh water of every kind, in brackish water, and water that contained more salt than sea water. Larvae which hatch out in fresh water die when placed in salt water, but those which hatch out in salt water live and develop into mosquitoes. The larvae are able to remain twenty minutes under water. In Madras this species breeds in both used and disused wells in the town; the authors found numbers of larvae in a well which was in constant use by no less than four families. In Mian Mir it breeds in tins of water.

Anopheles (*Cellia*) *pulcherrima*, Theobald. Palpi brown with four white bands, the apical one broad and including the tip. Thorax dark, with three longitudinal rows of white scales. Legs dark and speckled, the last three and a half and sometimes three and three-quarters of the hind tarsal segments entirely white. Costa with six black spots, the basal ones small. Egg much the same as that of *stephensi*, but the rim is much broader. Larva with simple and unbranched frontal hairs. Palmate hairs absent from the thorax; leaflets moderately long, the filament very long. This species is common in many parts of the Punjab, the North-West Frontier, and the Bombay Presidency. The larvae have been found in rain pools.

Anopheles (*Myzorhynchus*) *barbirostris*, Van der Wulp. Palpi dark, heavily clothed with scales, but without bands. Thorax dark, with some silvery scales. Abdomen brown. Legs dark brown without any true bands. Costa with a small patch of white scales at the junction of the apical and middle thirds, and another at the apex. Larva with a branched hair on the inner side of the antenna; median frontal hairs simple, occasionally forked; external hair branched, forming a cockade. Palmate hairs present on the second to the seventh segments; leaflets short and broad, filament short. This species is found scantily in most parts of the plains of India; Christophers records it as occurring in swarms in the forest regions of the Andaman Islands, where it attacked viciously. It seems hardly ever to come into houses, and may be considered a sylvan species.

Anopheles (*Myzorhynchus*) *sinensis*, Wiedemann. Palpi dark with four white bands, the apical one including the tip. Thorax dark, clothed with yellowish scales. Abdomen covered with yellowish hairs. Legs brown with small white bands at all the joints. Costa almost entirely black, except for two small white spots, one at the junction of the middle and apical third, the other near the apex of the wing. Larva with the median frontal hair forked, external hairs branched and forming a cockade; the antenna has a large branched hair on the inner side; palmate hairs are only present on the abdomen; leaflet long, lance-shaped and serrated, filament short and stout. This species is common in Bengal, Punjab, Bombay, and the Madras Presidency. The larvae are generally found in pools of water away from houses. According to James and Liston, *Anopheles* (*Myzorhynchus*) *nigerrimus* is identical with *sinensis*.

Anopheles (*Neocellia*) *fowleri*, Christophers. Palpi black with a broad apical band, and two narrow pale bands dividing the palps into three equal areas. Thorax black, covered with creamy white scales arranged in rows. Abdomen clothed with light coloured hairs and creamy white scales. Legs brownish, first to third tarsal segments of fore legs apically banded, the last two segments black. Pale bands on apex of first two tarsal segments of mid legs, the last three segments dark. Costa with four dark spots, the third from the apex of the wing the longest, and two small basal spots. This species resembles *fuliginosus*, but is of a lighter colour. Its larva also resembles that of *fuliginosus*, but the median frontal hairs are more branched. Palmate hairs absent on the thorax and the first abdominal segment; the second has undeveloped ones. The filament is half the length of the stem of the leaflet. The larvae are found in rice-fields, in borrow pits and in tanks, but not in flowing water. The imagines are very common in certain parts of the Central Provinces during the cold weather.

Anopheles (*Christophersia*) *halli*, James. Palpi clothed with white scales, forming five broad white bands, separated by four narrow black bands. Thorax brown with dark eye-like spots. Abdomen light brown. Legs dark and speckled with clear white spots; the third, fourth and fifth hind tarsi have white basal and apical bands. Costa with five distinct black spots, and some small indistinct ones near the base. This species is found in Sylhet, Assam. Its larva has a stumpy appearance; the median frontal hairs are simple and widely separated; the external ones are simple and very short, arising from papillae close to the bases of the median hairs. Palmate hairs present on third to seventh segments; leaflet of moderate length.

MALAYAN AND PHILIPPINE SPECIES OF ANOPHELES

Anopheles (*Stethomyia*) *fragilis*, Theobald. Palpi dark and without bands. Thorax brown. Abdomen brown or almost black. Legs brown and unbanded. Costa dark without spots. A small species found in the jungles near Kuala Lumpur, Federated Malay States. It breeds in jungle pools, and has a resting attitude like that of *Culex*.

Anopheles (*Myzorhynchus; Patagiamyia*) *separatus*, Leicester. Palpi with three white bands, the basal ones indistinct, the apical one including the tip. Thorax brown. Abdomen brown. Legs brown with indistinct bands at first three tarsal joints. Costa with two small spots. From Kuala Lumpur.

Anopheles (*Myzorhynchus*) *peditaeniatus*, Leicester. From the Malay States; considered by James and Stanton to be a variety of *sinensis* (see page 236).

Anopheles (*Myzorhynchus*) *minutus*, Theobald. From the Malay States and India, also considered by James and Liston to be a variety of *sinensis*.

Anopheles (*Lophoscelomyia*) *asiaticus*, Leicester. Palpi dark, unbanded. Thorax brown. Abdomen greenish yellow. Legs brown with a characteristic tuft of long scales at the joint between the hind femora and tibiae. Costa with two well-marked yellow spots. From Kuala Lumpur.

Anopheles (*Myzomyia*) *albirostris*, Theobald. Palpi with two broad yellowish white apical bands, and a much narrower one at the basal third. Thorax slate grey in middle, brown at sides. Abdomen brown with golden hairs. Legs brown with minute spots at the joints. Costa of wing black with three almost equal yellow spots, and a very small one near the base. From the Malay States. According to James and Stanton, it is a common species on some of the rubber plantations at Kuala Lumpur, where it has been found naturally infected with the parasites of malaria.

Anopheles (*Myzorhynchus*) *albotaeniatus*, Theobald. From the Malayan Region. It is similar to *albirostris* but said to differ from it as follows:—the first segment of the hind tarsus has narrow white basal and apical bands, the second and third are broadly banded at both ends, and the last tarsus is entirely white. It is found at Perak.

Anopheles (*Myzomyia*) *deceptor*, Dönitz. Palpi white from about the middle of the second joint, with dark rings at the bases of the third and fourth joints. Costa with four dark spots, and a very small fifth one at the base of the wing. From Sumatra.

Another species *A.* (*Myzomyia*) *leuchophyrus*, Dönitz, is in all probability the Indian *elegans*.

Anopheles (*Cellia*) *kochi*, Dönitz. Palpi yellow and black at the base, followed by a small ring of white and black scales, then a band of yellow followed by two broad bands of white, the last joint being pale yellow. Thorax pale brown with frosty tomentum. Abdomen brown with golden hairs. Legs speckled, and banded, last three tarsi of the fore and hind legs yellow. Costa with four black spots. From Malay and the adjacent parts.

Anopheles (*Cellia*) *punctulatus*, Dönitz. Almost identical with *kochi*, and only differing in having the tarsi clearly banded. From Malay and the adjacent parts.

Anopheles (*Stethomyia*) *pallida*, Ludlow. Palpi unbanded, wings without spots, but in all other respects like *A. fragilis* (see above); the thorax is said to have a frosty grey tomentum.

Anopheles (*Stethomyia*) *formosus*, Ludlow. Palpi brown with three white narrow pale bands, the apical one including the tip. Thorax with yellowish stripes. Abdomen greyish brown with light yellow hairs. Legs brown with narrow bands at the tarsal joints. Costa with four brown spots, the two at the base being smaller. From the Philippine Islands.

Anopheles (*Myzomyia*) *thorntoni*, Ludlow. Palpi with four white bands, the basal one narrow, the apical one broad and including the tip. Costa with four black spots and one or two minute ones at base. From Mindanoa, in the Philippine Islands. It is related to the Indian *elegans* (see page 228).

Anopheles (*Pyretophorus*) *minimus*, Theobald. Palpi with four white bands. Legs brown and unbanded. Costa black with three distinct almost equal yellow spots. From the Philippine Islands and China.

Anopheles (*Nyssorhynchus*) *philippinensis*, Ludlow. Palpi with four white bands, the apical one including the tip. Legs unbanded. Costa with two small and four large brown spots. From the Philippine Islands. This species comes very near the Indian *fuliginosus*, only differing in the markings on the wings and the absence of speckling on the legs.

Anopheles (*Pyretophorus*) *freerae*, Banks. Palpi with two white bands, one including the tip, and often a few pale spots near the base. Fore and mid legs with banded tarsi; posterior tarsi snow white. From Manilla.

Anopheles (*Calvertina*) *lineatus*, Ludlow. Palpi with three white bands, the apical one including the tip. Legs dark, hind metatarsus with a white spot at its apex, the next segment has a broad white apical band, and all the remaining joints are pure white. Costa with four small white spots, and a smaller fifth one at the tip. From the Philippine Islands.

Anopheles (*Cellia; Nyssorhynchus*) *flavus*, Ludlow. Palpi almost white with four yellowish bands, the apical one broad, and including the tip. Costa with seven or eight dark brown spots, four of which are large, and two basal ones. From the Philippine Islands.

Anopheles (sensu restricto) *treacheri*, Leicester. Said by James and Stanton to be identical with the Indian *aitkeni* (see page 228).

Anopheles (*Myzomyia*) *aurirostris*, Watson. Palpi brown with four white bands. Thorax and abdomen brown. Legs brown and unbanded. A small species from the Federated Malay States.

Anopheles (*Nyssorhynchus*) *nivipes*, Theobald. Palpi brown with two white bands or patches on ventral surface. James and Stanton record having seen the female, though up to the present the male alone has been described. According to these observers it is closely related to the Indian *fuliginosus*; it is found in Malay. Christophers records a local variety from the Andaman Islands, and has found its larvae in rice fields close to a sea embankment.

AUSTRALIAN SPECIES OF ANOPHELES

Anopheles (*Nyossrhynchus*) *annulipes*, Walker. Palpi brown, with four white bands, the proximal one broad, the basal narrow. Thorax of a slate brown colour with a central line of yellowish scales. Abdomen brownish black, clothed with yellow hairs. Tarsi with apical and basal pale bands. Costa with four black spots. Widely distributed in Australia and Tasmania, where it is believed to be the chief natural carrier of the parasites of malaria. It is also found in Formosa, where Kinoshita has demonstrated that it is suitable host for the parasites of malaria.

Anopheles (*Myzorhynchus*) *bancrofti*, Giles. Palpi black and unbanded. Thorax black with golden brown scales. Abdomen black with brown scales. Legs black, the tarsi with small apical pale bands. Costa black with two white spots. A large dark species widely distributed in Queensland.

Anopheles (sensu restricto) *corethroides*, Theobald. Palpi dark brown and unbanded. Thorax pale brown with a large median dark area in front. Abdomen deep brown. Legs brown and unbanded. Costa without any spots. This species is found in South Queensland.

Anopheles (sensu restricto) *atratus*, Skuse. Palpi dark, with light patches at the apices. Costa with six dark spots. Legs unbanded. It is found in South Queensland.

ARABIAN SPECIES OF ANOPHELES

Anopheles (sensu restricto ?) *arabiensis*, Patton. Palpi with three white bands, the distal one including the apex. Thorax brown. Abdomen clothed with brown hairs. Legs dark brown with yellowish bands at all joints. Costa with seven dark spots, four long and three short. Egg boat-shaped, frill well marked, the floats not encroaching on it. Larva with simple and unbranched frontal hairs; palmate hairs present on the second to the seventh segments; the leaflet is long and serrated, the filament long and pointed.

This species is extremely common in the Aden Hinterland, breeding in pools and along the edges of the smaller rivulets; it is also common near Sheik Othman, nine miles from Aden, where it breeds in wells. It was found by the senior author to be naturally infected with the sporozoits of the parasite of malaria. Mr. Theobald states that it does not belong to any of his genera, but up to the present he has not created a new genus for its reception. The type of this species and of the others described below were unfortunately lost with some baggage in the Aden Hinterland.

Anopheles (*Myzomyia*) *d'thali*, Patton. Palpi with two white bands. Thorax yellowish brown. Abdomen greenish with dark patches. Legs brown, faint bands at all the joints. Costa with four black spots, the basal one the longest. Egg boat-shaped with a narrow frill deeply encroached upon by the floats, which almost meet in the middle line. Larva with simple and unbranched frontal hairs; palmate hairs well developed from first to seventh segments; leaflet long and serrated more on one side than the other, filament long. Mr. Theobald thinks it is *Anopheles nili*.

Anopheles (*Nyssorhynchus*) *tibani*, Patton. Palpi with three white bands, the apical one broad and sometimes divided into two. Thorax dark with silvery scales. Abdomen clothed with dark hairs. Legs dark and banded, two and a half to two and three-quarters hind tarsi pure white. Costa with six white spots, the median one the longest. Egg with a narrow frill, floats extending up to it but not encroaching on it. Larva with simple and unbranched frontal hairs; palmate hairs from the second to the seventh segments; leaflet serrated more on one side than on the other, filament long. It breeds in all the rivers and springs in the Aden Hinterland, as far up as Jehaf (6,800 feet), and about ninety miles inland from Aden.

Anopheles (*Myzomyia*) *jehafi*, Patton. Palpi with four white bands, the last including the apex. Thorax and abdomen brown. Legs brown with pale areas at all the joints. Costa with six black spots. Egg boat-shaped, without a frill or floats, and thus unlike the typical anopheline egg; like that of *Stegomyia*, it will hatch after sinking in water. Larva with simple and unbranched frontal hairs; palmate hairs present on the third to the seventh segments; leaflet long, deeply serrated; filament long and pointed. This species breeds in springs and wells.

Anopheles (*Myzomyia*) *azriki*, Patton. Palpi with three bands, apices dark. Thorax and abdomen brown. Legs brown, without bands. Costa with five black spots. Larva with simple and unbranched frontal hairs; palmate hairs present on fourth to seventh segments; leaflet short and broad, and serrated; filament with a short spike. It was found in the Aden Hinterland, breeding in a spring.

European Species of Anopheles

Anopheles (sensu restricto) *maculipennis*, Meigen. Palpi brown, unbanded. Thorax and abdomen brown. Legs brown, without any definite bands. Costa dark with four dark spots, two apical and two median. It is widely distributed in Europe, and is a natural carrier of the parasites of malaria in Italy.

Anopheles (sensu restricto) *bifurcatus*, L. Palpi unbanded. Thorax chestnut brown. Abdomen dark brown, with some short golden hairs. Legs brown and unbanded. Costa and wing itself without any spots. Europe.

Anopheles (sensu restricto) *nigripes*, Staeger. Palpi black and unbanded, but sometimes with traces of light bands. Thorax and abdomen blackish brown. Legs deep brown, without bands. Costa black without spots. Europe.

Anopheles (*Myzorhynchus*) *pseudopictus*, Grassi. Palpi brown, with three white-scaled bands. Thorax and abdomen dark. Legs brown, apices of metatarsi and tarsi with narrow pale bands. Costa with two light spots at its apex. Italy and some other parts of Europe.

Anopheles (*Myzomyia*) *hispaniola*, Theobald, and *Anopheles* (*Pyretophorus* ?) *superpictus*, Grassi, from Spain and the neighbouring Islands, and from Southern Europe, are described on pages 250 and 251.

Anopheles (*Pyretophorus*) *cardamatisi*, Newstead and Carter. Palpi long and thin, with three white bands, the apical one of which is the broadest. Thorax greyish brown with whitish scales. Abdomen brown with pale hairs. Legs brown with light markings at the joints. Costa with six black spots, the three basal ones small. From Athens.

NORTH AMERICAN SPECIES OF ANOPHELES

Anopheles (sensu restricto) *punctipennis*, Say. Palpi with two indistinct greyish bands, and apices sometimes grey. Thorax chestnut brown. Abdomen brown with golden hairs. Legs brown, except coxae, knees and tips of tibiae, which are yellowish. Costa black, with two yellow spots, one at the apex and the other at the apical third. This species is the winter anopheline of the United States.

Anopheles (sensu restricto) *perplexans*, Ludlow. Palpi dark with white tips. Thorax with a broad white median stripe, and covered with white frost. Abdomen dark brown. Legs with extremities of femora and tibiae yellowish. Costa with one small yellowish spot, and a second one at its junction with the first longitudinal vein. From Pennsylvania.

Anopheles (sensu restricto) *franciscanus*, McCracken. Palpi with three indistinct pale bands. Legs without any distinct bands. Costa with two yellow spots. From California and Texas.

Anopheles (sensu restricto) *crucians*, Wied. Palpi with three white bands, the last one including the apex, which is silvery grey. Legs brown, with tips of femora and tibiae yellowish. Costa with one yellow spot. Widely distributed in North America, where it is a common species.

Anopheles (sensu restricto) *barberi*, Coquillett. This is the 'tree-hole' anopheline of the United States; it commonly breeds in the water which collects in hollow trees. Theobald thinks it is very near the European *bifurcatus* (page 241). It is found in Maryland and New Jersey.

Anopheles (sensu restricto) *occidentalis*, Dyar and Knab. Palpi, abdomen, and legs, brown. Thorax with a broad band on dorsum, cut across by three narrow stripes. Wing with four black spots. From California, San Diego, and Oregon.

Anopheles (sensu restricto) *atropos*, Dyar and Knab, and *Anopheles* (sensu restricto) *quadrimaculatus*, Say, are probably only varieties of *A. maculipennis*.

In addition to the above, *A. maculipennis*, *A. bifurcatus*, and *A. nivipes* are found in parts of North America.

AFRICAN SPECIES OF ANOPHELES

EDWARD'S KEY TO THE SPECIES

1. Thorax with distinct broadish-elliptical scales (except in *A. christyi*); female palpi shaggily scaled; abdomen usually more or less scaly 2
Thorax clothed with hairs, or narrow almost hair-like scales; scales of female palpi usually appressed; abdomen without scales on the dorsal surface 13

2. Abdominal scales obviously present on all the segments 3
Abdominal scales absent, or if present, confined to the terminal segments ('*Nyssorhynchus*') 8

3. Abdominal scales forming distinct projecting lateral tufts (*Nyssorhynchus*, [=*Cellia*]) 4
Abdominal scales not forming tufts (*Neocellia*) 9

4. Last joint of hind tarsi light, or at least light-tipped 5
Last joint of all tarsi entirely dark 7

5. Last joint of fore and mid tarsi all dark; rather light yellowish species (5 to 6 mm) . . . . **pharoensis.**
Last joint of fore and mid tarsi light or light-tipped; smaller, less yellow species (4.5 mm. or less) 6

6. Last joint of all tarsi wholly yellow; remaining joints regularly ringed with black and yellow; very small species (3 mm) . . . . **cinctus.**
Last joint of all tarsi white tipped; remaining joints not ringed; larger species . . . . **jacobi.**

7. Hind tarsi entirely dark . . . . **argenteolobatus.**
First four joints of hind tarsi with equal white rings . . **squamosus.**

8. Last tarsal joint white; small species (3.5 mm); Egyptian . **maculicosta.**
Last tarsal joint not white; large species (7 mm); East African . . . . **christyi.**

9. Hind tarsi entirely dark; three white palpal bands in female, the first two narrow . . . . **brunnipes.**
Last two or three joints of hind tarsi white 10

10. Four narrow white palpal bands; wing scales lanceolate; legs spotted . . . . **aureosquamiger**

Three palpal bands, the two last rather broad; wing scales much narrower . . . 11
11. Femora and tibiae white-spotted . . . 12
Femora and tibiae not white-spotted . . . **rufipes.**
12. Palpi white-spotted . . . **maculipalpis.**
Palpi not white-spotted . . . **pretoriensis.**
13. Abdomen with lateral tufts of very long slender scales on each segment (*Christya*) . . . **implexus.**
Abdomen without lateral scale tufts . . . 14
14. Wing scales mostly yellow, the black patches on the veins much reduced, but three long and one short black marks on the costa and first vein, the first two almost or quite united . . . 15
Wings not so marked . . . 16
15. Last 2¾ joints of hind tarsi white . . . **theileri.**
Last joint of hind tarsi dark . . . **wellcomei.**
16. Wings with at least three pale spots on the costal border (doubtful species are included in the next division, [*Myzomyia*]) . . . 17
Wings with at most two pale spots on the costal border . . . 36
17. Last hind tarsal joints white; legs spotted . . . **natalensis.**
Last hind tarsal joints not white . . . 18
18. Femora and tibiae more or less spotted with white; tarsi distinctly ringed at the joints . . . 19
Femora and tibiae not at all white-spotted . . . 20
19. Hind metatarsi with about five well-marked narrow whitish rings; female palpi with four narrow white rings . . . **ardensis.**
Hind metatarsi without distinct rings; female palpi with three white rings, the apical one broad . . . **costalis.**
20. Third vein with three dark and two light areas; male palpi with the club mainly yellow, as in *costalis* . . . **pallidopalpis.**
Third vein with only two dark areas (near base and apex), or entirely dark . . . 21
21. Palpi of female white only at the apex; base of first fork-cell nearer apex of wing than that of second; small, very dark species . . . **nili.**
Palpi of female with three or four white rings . . . 22
22. Third vein mainly, (*funestus*, type form, and *culicifacies*) or entirely dark; mesonotum clothed with hairs . . . 23
Third vein mainly pale . . . 26
23. Hind tarsi with fairly distinct pale rings; wing field with some pale spots . . . **longipalpis.**
Legs entirely dark . . . 24
24. Wing field entirely dark; no pale scales even at bases of fork-cells . . . **rhodesiensis.**
Pale spots present at bases of fork-cells, even in the darkest specimens . . . 25
25. Lighter species, Mediterranean and Oriental . . . **culicifacies.**
Darker species (very variable), Ethiopian . . . **funestus.**
26. Palpi of female black-tipped . . . 27
Palpi of female white-tipped (in *A. cinereus* the white scales at the tip are easily rubbed off); mesonotum with narrow, but fairly distinct scales . . . 30

27.	No dark scales on first fork-cell or on anterior branch of second	**impunctus.**
	Dark spots present (though sometimes small) on first fork-cell	28
28.	Vestiture of mesonotum consists of hairs	**hispaniola.**
	Vestiture of mesonotum consists of narrow scales	29
29.	Third and fourth costal spots smaller; first fork-cell mainly pale-scaled	**chaudoyei.**
	Third and fourth costal spots larger; first fork-cell mainly dark-scaled	**multicolor.**
30.	Last joint of female palpi mainly dark, pale at each end; large species, wing length about 5 mm.	**cinereus.**
	Last joint of female palpi mainly or entirely white	31
31.	Tarsi dark; middle ring on female palpi rather narrow	32
	Tarsi with pale articulations	33
32.	Average wing length 3.8 mm.	**transvaalensis.**
	Average wing length 3 mm.	**funestus.**
33.	Larger (about 5 mm.); Mediterranean	**superpictus.**
	Smaller; Ethiopian; middle and terminal pale rings on female palpi about equal and rather broad; tarsal joints with narrow yellowish rings	34
34.	Larger, darker species (3.5 to 4.5 mm); third and fourth costal spots larger	**marshalli.**
	Smaller, lighter species (3 to 3.2 mm); third and fourth costal spots smaller	35
35.	A dark spot at apex of wing	**pitchfordi.**
	No dark spot at apex of wing	**flavicosta.**
36.	Thorax clothed with narrow scales; light spots on wing more numerous	37
	Thorax clothed with hairs (excluding the scales near the front margin); wings very dark, or else quite unicolourous	39
37.	The two last palpal bands (in female) about equal and rather broad—as in *marshalli*; tarsal joints with rather broad white apical rings	**austeni.**
	Palpi of female with four narrow whitish rings; the terminal joint having a dark ring in the middle	38
38.	Numerous yellow-forked scales on the head; legs dark, tarsi scarcely ringed	**distinctus.**
	No yellow-forked scales on head; femora and tibiae spotted with whitish, tarsi distinctly ringed at the joints	**costalis** var. **melas.**
39.	Last 2 to 3 joints of hind tarsi white; female with a tuft of scales on the ventral side of the last abdominal segment (*Myzorhynchus*)	**muritianus.**
	Last joints of hind tarsi not white; female without ventral scale-tuft	40
40.	Blackish species; wings with some pale spots	41
	Lighter species; wings without any pale spots	42
41.	Female palpi shaggily scaled; pale scales of wings occurring mainly on the fourth, fifth and sixth veins	**umbrosus.**
	Female palpi with appressed scales; pale scales of wings less numerous and occurring mainly on the first vein	**smithii.**
42.	Wings with dark spots formed by accumulation of scales.	**maculipennis.**

Wings without any dark spots **43**

43. First fork-cell longer than the second . . . . **algeriensis.**

Fork-cells of equal length . . . . **antennatus.**

Anopheles (*Cellia*) *pharoensis*, Theobald. Palpi brown with two narrow white bands, and white tip, elsewhere mottled with white. Thorax brown, with a dark median line and a fawn coloured stripe on each side; abdomen brown, densely covered with yellowish hairs and scales, and with lateral tufts of darker scales. Legs with femora and tibiae banded and mottled, metatarsi and tarsi with broad apical white bands; last tarsal joint white. Costa with three dark spots, the middle one the largest, the two others small. A distinct and very widely distributed African species. Recorded from Palestine, Egypt, Soudan, Gambia, North and South Nigeria, Togo Land, the Belgian Cogo, Angola, Southern Rhodesia, Delogoa Bay, and Madagascar.

Anopheles (*Cellia*) *cinctus*, Newstead and Carter. Distinguished from the above and allied forms by the rings on the metatarsi of the middle and hind legs; only one specimen is known, from Ashanti.

Anopheles (*Cellia*) *jacobi*, Hill and Haddon. A large black and white species with spotted legs. Palpi black, with an incomplete white band near the base, a narrow band about the middle, and an irregular white band at apex. Thorax sepia with three white longitudinal bands, as well as three on pleura. Abdomen thickly covered with yellow scales and hairs, and with lateral tufts of black scales on second to seventh segments. Legs dark grey, spotted with white; metatarsi and all tarsi except the third of the fore and mid legs with white bands; the last tarsi of all legs white. Costa with three small white spots, a fourth at the apex, and two small spots at the base. The larva, which lives in springs, is large and deeply pigmented; antenna without a branched hair on the shaft, but with a small spine on the external aspect. Frontal hairs branched; palmate hairs absent on thorax, rudimentary on first abdominal segment, better developed on second, and prominent on third to seventh segments; leaflet broad. This species is found in South Africa.

Anopheles (*Cellia*) *argenteolobatus*, Gough. Palpi dark, with three white bands. Thorax dark, with a large eye-like spot on each side of the median line. Abdomen dark brown. Legs brown, unbanded. Costa black with three large white spots and two smaller ones. It is found in the Transvaal and North-East Rhodesia. Edwards considers that *Anopheles pseudosquamosus*, Newst. and Cart., is identical with it.

Anopheles (*Cellia*) *squamosus*, Theobald. Palpi dark, with two narrow white bands and white apex. Thorax dark, with white scales arranged in lines; pleura with three white lines. Legs dark, speckled with white; apex of first and second tarsal joints of fore and mid legs with broad white bands; metatarsi of hind legs with apical bands, as well as the next three tarsal joints, the last black. Costa jet black, with three distinct white spots, one smaller at apex and two at base. This is a dark species, widely distributed in Africa; it has been recorded from Egypt, Sudan, Northern Nigeria, Sierra Leone, Gold Coast, Angola, Natal, Transvaal, Rhodesia, Nyasaland and British East Africa; it also occurs in Madagascar.

Its larva is slender with a pigmented median stripe. Antenna without a branched hair, terminal spines equal. Frontal hairs consisting of three pairs, the external dendriform. Palmate hairs rudimentary on the thorax, well developed on the first abdominal segment, large on the second to seventh; leaflets narrow and few in number. The larvae are found in springs and marshes.

Anopheles (*Cellia*) *maculicosta*, Becker. This species is considered by Edwards to be a worn specimen of *A. pharoensis*. From Egypt.

Anopheles (*Neocellia*) *christyi*, Newstead and Carter. Palpi brown with two white apical bands, and a narrow creamy basal one. Thorax almost black, with cream coloured scales. Abdomen very dark, with white basal lateral areas to the middle segments. Legs brown: tarsi of fore and hind legs dark with broad apical creamy bands, the last segment dark. Costa with five black spots, the second and third the longest. Wing unusually broad. It is found in Uganda and British East Africa.

Anopheles (*Nyssorhynchus*) *brunnipes*, Theobald. Palpi black, with two narrow white apical bands and broad white tip. Thorax brown, with a dark median line, narrow submedian lines, and two dark spots. Legs uniformly brown. Costa dark with three large creamy white spots, and two smaller ones near base; the first fork-cell is very long. From Angola.

Anopheles (*Pyretophorus*) *aureosquamiger*, Theobald. Palpi brown, with four white bands, one apical and the others lower down. Thorax slate grey with characteristic golden spindle-shaped scales. Abdomen blackish brown. Legs brown with spots; first two tarsi of fore leg with broad white apical band, the last three of the hind leg entirely white. From the Transvaal.

Anopheles (*Nyssorhynchus*) *rufipes*, Gough. Palpi without spots, but with two pale apical bands. Hind legs with narrow white bands, apices of tibiae, metatarsi, and first tarsal joints, also third to fifth tarsal joints, white; black band near base of third. This species is closely related to *A. pretoriensis.* It is found in British East Africa, Gold Coast, North and South Nigeria.

Anopheles (Nyssorhynchus) maculipalpis, Giles. According to Edwards, who has re-examined the British Museum specimens, this species is identical with the Indian anophelene bearing the same name (see page 233). It is widely distributed, and is recorded from the Transvaal Rhodesia, Congo and Nigeria.

Anopheles (*Nyssorhynchus*) *pretoriensis,* Theobald. This species closely resembles *maculipalpis,* except that the palpi are not mottled with white, and the bands are further apart; the last two tarsi of the hind leg are all white. The larva is said to differ from that of *maculipalpis* in having the frontal hairs unbranched, the outer very short and the median long and thin. It is found in the Transvaal and Natal.

Anopheles (*Christya*) *implexus,* Theobald. A large species. Palpi with three white bands, and white apices. Thorax brown with golden yellow scales. Abdomen black with long dense lateral tufts of black and golden hairs, the black ones in apical tufts. Legs brown, femora and tibiae spotted, third and fourth segments of hind tarsi white, the last segment black. A very striking *Anopheles,* for which Theobald erected the genus *Christya,* of which it is the only species.

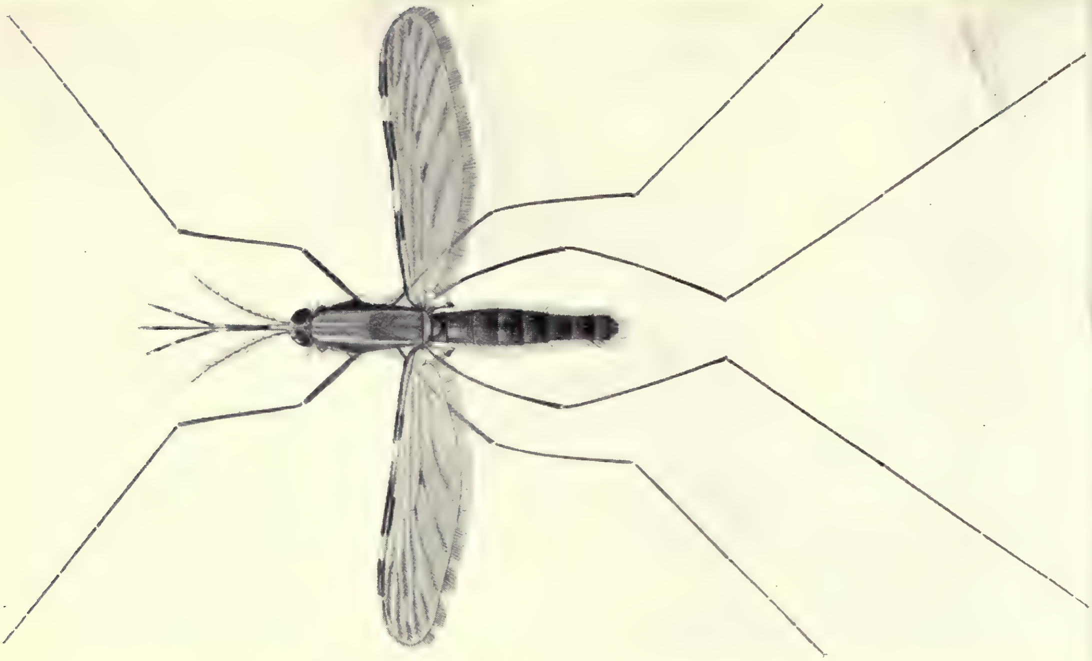
Anopheles (*Pyretophorus*) *thelleri,* Edwards (*P. albipes,* Theobald). No description is given, but it is said to be a very distinct species, but in its wing markings almost identical with *A. wellcomei* (?) Theobald (see below). It is found in the Transvaal.

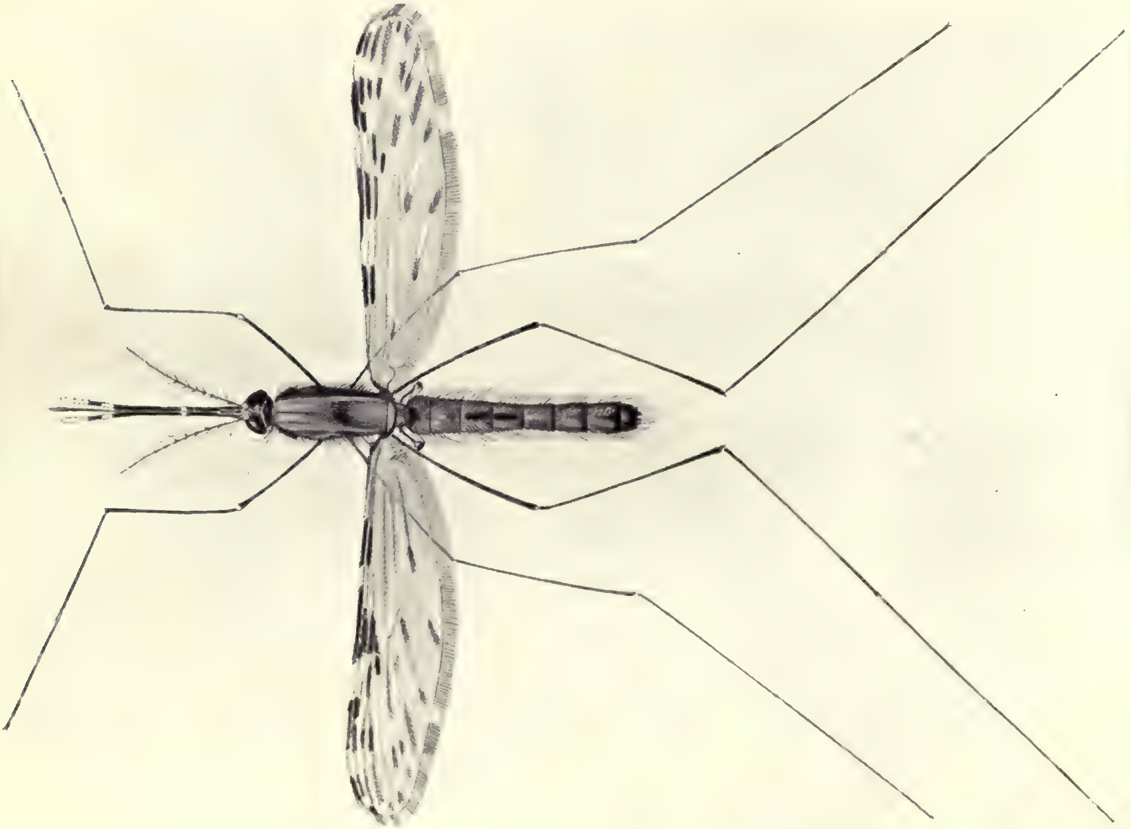
Anopheles (sensu restricto) *wellcomei,* Theobald. Palpi with two white bands, one near the apex, and the other about one-fourth the way down. Thorax ash grey with a broad dark median stripe. Abdomen ochreous. Legs brown with very narrow yellow apical bands. Costa with two well marked yellow spots near the apex. From the Soudan, Northern Nigeria, and Angola.

Anopheles (*Myzorhnchus*) *natalensis,* Hill and Haddon. Palpi with five pale bands including the apex. Costa with three white spots and a fourth at the apex. Legs spotted and banded. First hind tarsi with broad apical bands, last tarsi two and a half to two and three quarters white. Natal.

Anopheles (*Pyretophorus*) *ardensis,* Theobald. Palpi with three narrow white bands and white apices. Thorax greyish brown. Legs brown, femora, tibiae, and metatarsi spotted, remaining tarsi with apical pale bands. It is found in Natal and is probably only a variety of *A. costalis.*

PLATE XXXIX





Anopheles (*Pyretophorus*) *costalis*, Loew. (Plate XXXIX, fig. 1.) Palpi with two white bands, and yellowish white apices; a variation is often seen in the band at the apex, which may be divided, the palp then appearing to have four bands. Thorax brown with a dusky median line, and when denuded of scales with five lines. Abdomen black with long golden hairs. Legs with femora and tibiae brown, spotted with white; the tarsal joints are banded with yellow, especially in the fore legs. Costa with four large and two small black spots, the two median ones the longest. This species is very widely distributed in Africa, as well as in Madagascar and Mauritius; it is a natural carrier of the parasites of malaria. The larva has branched frontal hairs; the antenna is without a lateral hair or plume on its shaft; the palmate hairs are present from the second to the seventh segments, each leaflet being filamentous. The larvae are commonly found in swampy water, in roadside puddles and in foul pools about African houses.

Anopheles costalis shows considerable variation in its markings, and the late Dr. Dönitz was of the opinion that Theobald's identification of the species is erroneous, and that it is probably *A. cinereus*, Theobald; he therefore suggested the name *gracilis*.

Anopheles (*Feltinella*) *pallidopalpi*, Theobald. Palpi with two yellow bands, one of which is apical. Thorax ash-grey with a median dark line. Abdomen brown with golden hairs. Legs brown, and unbanded. Costa with two pale spots. The genus *Feltinella* was created on the character of the male genitalia, the basal lobe, according to Theobald, being divided into two segments. Edwards states that 'the type specimen is merely broken.' This species, of which only the male is known, is found in Sierra Leone.

Anopheles (*Myzomyia*) *nili*, Theobald. Palpi dark, with one small apical band. Thorax fawn coloured. Abdomen black. Legs brown, and unbanded. Costa black, with three yellow spots. From the Soudan, North and South Nigeria, and Togo Land.

Anopheles (*Myzomyia*) *longipalpis*, Theobald. Palpi with three narrow white bands, and white apices. Thorax cinerous. Abdomen black. Legs black, hind tarsi and metatarsi with apical and basal yellow bands. Costa dark with four almost equal pale yellow spots. From British East Africa, and Nyasaland.

Anopheles (*Myzomyia*) *rhodesiensis*, Theobald. Palpi dark brown with three narrow yellow apical bands. Thorax reddish brown. Abdomen brown. Legs dark brown, long and thin, and unbanded, Costa with three small white spots, and a yellow spot at apex. This species is found in Southern Rhodesia, and in the Transvaal. Edwards states that it is often confused with *Anopheles funestus*.

Anopheles (Myzomyia) culicifacies, Giles. Edwards states that, after examining a large series of typical *culicifacies* from India, he regards *A. (Pyretophorus) sergenti*, Theobald, as a synonym. For a description of *culicifacies*, see page 229. It is found in parts of Algeria.

Anopheles (Myzomyia) funestus, Giles. (Plate XXXIX, fig. 2.) Palpi with two white bands and white apices. Thorax dark brown at sides and grey in middle. Abdomen blackish brown with light hairs. Legs dark brown, metatarsi and tarsi with narrow apical bands, which are often absent. Costa with four small yellowish spots, and sometimes two smaller ones. Several varieties have been described; *A. hebes*, Dönitz, is probably only a variety, and Edwards states that it only differs from the type *funestus* in having narrower wings, and pale scales on half of the third vein. The variety *subumbrosa*, Theobald, has no pale spots on the costa near the base, but has some pale scales in the middle of the third vein; the fringe spots are usually distinct. According to Edwards, the species *A. (Myzomyia) leptomeres*, Theobald, is this variety. The variety *bisignata*, Grünberg, has no pale spot near the base of the costa, the third vein and sometimes also the fifth are entirely dark, and the fringe spots are indistinct or absent.

Anopheles funestus is widely distributed in Africa, being commonest in West Africa; it is a natural carrier of the parasites of malaria. The larva has branched frontal hairs; no hair on the shaft of the antenna. The palmate hairs, which are present from the second to the seventh segments, are filamentous. They are nearly always found in clear water, never in marshy or foul pools.

Anopheles (Myzomyia) impunctus, Dönitz. A little known species and of doubtful position; one specimen was obtained from Egypt.

Anopheles (Myzomyia) hispaniola, Theobald. Palpi brown with three pale bands, the apical one being very small, the greater part of the apical joint black. Thorax slate-grey with brown sides. Abdomen blackish brown, paler below. Legs brown, apices of femora and tibiae pale yellow, tarsi unbanded. Costa with five black spots, the basal part being black. Edwards states that *A. (Pyretophorus) myzomyfacies*, Theobald, is a synonym. It is found in Spain, Algeria, and the neighbouring parts.

Anopheles (Pyretophorus) chaudoyei, Theobald. Palpi with three narrow white bands, the first two nearer one another than the second and with two indistinct median lines. Abdomen dark brown, nearly black. Legs brown with traces of bands on the fore and mid tibiae. Costa mostly pale, with five or six black spots, all smaller than the intervening clear spaces. According to Edwards *A.* (*Pyretophorus*) *nigrifasciatus*, Theobald, is a synonym (see page 231). *A. chaudoyei* is found in Algeria and Cyprus.

Anopheles (sensu restricto) *multicolor*, Camboulin. A doubtful species described from Suez and Cairo.

Anopheles (*Pyretophorus*) *cinereus*, Theobald. Palpi with four white bands, the terminal ones including the apices. Thorax ash grey in the middle and dark brown at the sides. Abdomen dark. Legs thin, dark, and spotted, last tarsal joints of all legs paler than the rest. Costa black with three yellow spots. From British East Africa, Rhodesia, Transvaal, Natal and the Cape.

Anopheles (*Pyretophorus*) *transvaalensis*, Carter. A doubtful species from East Africa, Transvaal and Natal. Edwards thinks it will probably prove to be *A. funestus*.

Anopheles (*Pyretophorus*) *superpictus*, Grassi. Palpi with three white bands, the apical joint and apex being entirely white. Thorax brown with light scales. Abdomen brownish yellow. Legs brown with white bands at most of the joints. Costa with four black spots, and one or more in addition near the base. It is found all over Southern Europe, and along the North African Coast.

Anopheles (*Pyretophorus*) *marshalli*, Theobald. Palpi black, with a white apical band, another of the same width close to it, and a smaller one near the base. Thorax slate grey, and brown at the sides. Abdomen black with golden hairs. Legs brown, apices of all joints except the last tarsal with small yellow bands. Costa with six small creamy spots. From Uganda, British East Africa, Nyasaland, Rhodesia, Angola, and the Transvaal.

Anopheles (*Pyretophorus*) *pitcpfordi*, Power, (in Giles). An imperfectly described species with four light spots on the costa. From Zululand and Uganda.

Anopheles (*Myzomyia*) *flavicosta*, Edwards. Palpi with three white bands, a narrow one near the base, the last, including the tip, broad, the intermediate band equally broad. Thorax ash grey with brown sides. Abdomen dark brown with golden yellow hair. Costa with four black spots, and black at the base. From Northern Nigeria.

Anopheles (*Pyretophorus*) *austeni*, Theobald. Palpi with two broad white bands, one forming the apex, and a much narrower third band.

Thorax brown with silvery scales. Abdomen black with golden hairs. Legs black with apices of all segments, except the last in the fore and mid legs, with narrow white bands. Costa with three white spots, the apical one large, the second smaller, and the third very small. From Angola.

Anopheles (*Pyretophorus*) *distinctus*, Newstead and Carter. Palpi with four white bands, the apices white. Thorax slate grey with a dark median longitudinal line. Abdomen dark brown, with pale golden brown hairs. Legs brown, lighter below; fore legs with narrow white apical bands on the metatarsus and first tarsal segments; middle and hind legs with pale areas at the articulations. Costa mostly black with two pale spots; these characters distinguish it from any other anopheline. From the Luapala river, North-East Rhodesia. A variety *melanocosta* is also recorded from the same locality, which differs from the type in having the whole of the costa black, with the exception of a small pale apical spot.

Anopheles (*Myzorhynchus*) *muritianus*, Grandpré. Palpi with four pale bands, the terminal one including the apex. Thorax dark brown with dark longitudinal lines. Abdomen black, clothed with brown hairs. Fore and mid tarsi with white bands at their apices, hind tarsi banded with white apically and basally; apex of first, most of the second, and both the last tarsi of the hind leg banded or entirely white. Costa black with two white spots, one near the apex. This species is widely distributed in Africa and is said to be the commonest anopheline at Nairobi.

Anopheles (*Myzorhynchus*) *umbrosus*, Theobald. Palpi black, without any bands. Thorax black with traces of lines and with golden scales. Abdomen grey with brown hairs. Legs brown, all joints with pale bands. Costa black with a yellow spot at the apex. Found in Southern Nigeria, Congo, Cameroon, and the Malay States. Edwards states that *A.* (*Myzorhynchus*) *obscurus*, Grünberg, and *A.* (*Myzorhynchus*) *strachani*, Theobald, are synonyms.

Anopheles (sensu restricto) *smithi*, Theobald. Palpi black with three narrow pale lands, apices black. Thorax grey with a dark median line. Abdomen black with brown hairs. Legs brown and unbanded. Costa black. From Sierra Leone.

Anopheles (sensu restricto) *maculipennis*, Meigen. This species is chiefly European and is described on page 241. It is said to occur in Tunis.

Anopheles (sensu restricto) *algeriensis*, Theobald. This species is probably identical with the European *bifurcatus*, (see page 241).

Anopheles (sensu restricto) *antennatus*, Becker. A species difficult to locate and placed as uncertain by Theobald.

SOUTH AMERICAN AND WEST INDIAN SPECIES OF ANOPHELES.

Anopheles (sensu restricto) *vestipennis*, Dyar and Knab. Tarsi banded with white, hind tarsi black and white. Costa with small yellow spots. An imperfectly described species, from Guatemala, Mexico.

Anopheles (sensu restricto) *strigumacula*, Dyar and Knab. Another doubtful species from Cordoba, Mexico.

Anopheles (sensu restricto) *apicimacula*, Dyar and Knab. Said to be like the former species, but with a distinct black costo-apical spot on wing. It is found in Guatemala, Panama and Trinidad.

Anopheles (sensu restricto) *punctimacula*, Dyar and Knab, from Colon, and *Anopheles eiseni* (?) Coquillett, from Guatemala are doubtful species.

Anopheles (sensu restricto) *pseudopunctipennis*, Theobald. Palpi with three white bands, the last one including the apex. Legs brown, coxae, trochanters and base of femora pale. Costa with two yellowish white spots. From Grenada.

Anopheles (*Stethomyia*) *nimbus*, Theobald. Palpi long and thin without any bands. Thorax black with a silvery median line. Legs long, thin, and unbanded. Wings densely scaled but unspotted. From British Guiana, also from Brazil. It simulates a *Culex* when at rest.

Anopheles (*Chagasia*) *fajardi*, Lutz. Palpi with dense dark scales and pale rings at the joints. Thorax yellowish white with golden sheen. Legs spotted and banded, the bands on the tarsi broad. Wings without any spots. When at rest assumes the attitude of *Culex*. Egg without floats, ribbed and striated. Larva with simple median frontal hairs, external pair branched; palmate hairs from first to seventh segments; leaflet broad, fan-like; filament with a simple hair projecting from centre. From Brazil.

Anopheles (*Myzorhynchella*; *Chagasia*) *niger*, Theobald. Palpi dark with four narrow white bands, the two apical ones close together. Thorax black with creamy-white scales. Legs banded, apex of hind metatarsus, half the second and the last three tarsi pure white. Costa with three small yellow spots and two smaller ones at base. From Mexico and Brazil.

Anopheles (*Myzorhynchella*; *Chagasia*) *nigritarsus*, Chagas. Palpi dark, without any distinct bands. Thorax and abdomen dark brown. Legs dark, with spots and bands, the last tarsus of hind leg pure white, the third and fourth white with black rings. Costa dark with five yellow spots. From Brazil.

Anopheles (*Myzorhynchella*; *Chagasia*) *lutzianus*, Chagas. Palpi black, with white scales at the apices of the segments. Legs dark, with spots and bands, the distal two-fifths of the second and the last three white. Costa dark with four yellow spots. From Brazil.

Anopheles (*Myzorhynchella*; *Chagasia*) *parvus*, *Chagas*. Palpi with four white bands, the terminal one including apex. The distal half of the second hind tarsi and the last three tarsi white. Costa with three small white spots. From Brazil.

Anopheles (*Myzorhynchella*) *tibiamaculatus*, Neiva. Palpi dark with about one-third of apical segment white. Legs spotted. Costa with two small yellow spots. From Brazil.

Anopheles (*Cyclolepidopteron*) *mediopunctatus*, Theobald. Palpi banded with black and gold. Thorax reddish brown with a green sheen, and two dark eye spots. Abdomen brown. Legs brown, with spots and bands, the last tarsal joints of all legs yellow. Costa with three well-marked black spots. From Brazil.

Anopheles (*Cyclolepidopteron*) *intermedius*, Chagas. Only differs from the above in having no bands on the palps.

Anopheles (*Arribalzagia*) *maculipes*, Theobald. Palpi with four white bands, the last one including the tip. Thorax brown with slate-grey sheen. Legs brown with many spots, and white bands. Costa with three black spots. From Brazil and Trinidad.

Anopheles (*Arribalzagia*) *pseudomaculipes*, Chagas. According to Chagas it differs from the above in having broader wing scales, and many more tarsal spots. From Brazil.

Anopheles (*Manguinhosia*) *lutzi*, Chagas. Palpi dark with indistinct stripes. Legs yellowish brown, ends of tibiae white. Costa with two large black spots, and one or more smaller ones. From Brazil.

Anopheles (*Kerteszia*) *boliviensis*, Theobald. Palpi with three narrow yellow bands, one of which forms the apex. Thorax ash grey, with two straight parallel median lines. Legs brown; two or three tarsal segments are spotted or banded. Costa with four yellow spots. From Bolivia.

Anopheles (*Myzomyia*) *lutzi*, Theobald. Palpi dark, with three narrow white bands, one of which is at the tip. Legs dark and banded, first tarsal segment of fore and mid legs banded with dark and white bands; the last three tarsi of fore and hind legs with white tips. Costa with five pale spots. Rio de Janeiro.

Anopheles (*Cellia*) ***bigotii***, Theobald. Palpi with four white bands, one at the apex. Thorax brown with four greyish longitudinal lines. Legs brown, banded; apical band on metatarsus and first two tarsi of fore legs, and last joint white; last three tarsi and apex of the first of the hind leg pure white. Costa dark with three white spots. From Chili.

Anopheles (*Cellia*) ***brasiliensis***, Peryassu. Allied to *argyrotarsis* (see below), but the three spots on the wing costa are larger. From Brazil.

Anopheles (sensu restricto) *mattogrossensis*, Lutz and Neiva. Palpi dark and unbanded. Thorax dark in the centre and yellowish at the sides. Abdomen dark with silvery hairs. Legs dark with a bronze sheen, with indistinct apical rings to the upper segments. Wing dark with two brownish yellow spots on the costa. From Lake Mandicore, Motto Grosso, Brazil.

Anopheles (*Cyclolepidopteron*) *grabhami*, Theobald. Palpi densely scaled, but unbanded. Thorax slate grey, mottled with brown. Legs brown and spotted. Costa black with a yellow spot at the tip of the wing. Larva with a characteristic white mark on its thorax; frontal hairs simple and unbranched; palmate hairs from second to seventh segments; leaflet long and without any definite filament. From Jamaica and Cuba.

Anopheles (*Cellia*) *argyrotarsis*, Robineau-Desvoidy. Palpi with three white bands, one including the apex. Legs yellowish, the apex of the first tarsus of the hind leg and the last three tarsi white. Costa with four large white patches and one or two smaller ones. This species is common in the West Indies, and is found in St. Lucia, Antigua, Grenada, Jamaica Cuba, Haitai, and Porto Rico; it is also recorded from British Guiana, Brazil, and the Argentine. It is an important natural carrier of the parasites of malaria.

Anopheles (*Cellia*) *aibimanus*, Wied. This species is almost indistinguishable from *argyrotarsis*, and can only be separated by noting that the last segment of the hind tarsus is entirely black, while, except for the claws, it is white in *argyrotarsis*. It is common in many parts of the West Indies, and in Brazil. It is a carrier of the parasites of malaria, and can also act as the host of *Filalria bancrofti*. It breeds in swamps, pools, and in almost any kind of water.

Bionomics of the Anophelina

In spite of the large number of observations which have been made during the course of investigations into the etiology of mosquito-borne diseases, it has to be admitted that our knowledge of the bionomics of the Anophelina, even in the case of definitely incriminated species, is far from complete.

The subject is a difficult one, for a large number of observations must be allowed to accumulate before reliable conclusions can be drawn, and workers in this field are severely handicapped by the difficulty which exists in imitating natural conditions sufficiently closely to enable one to carry out prolonged and exact experiments with mosquitoes in captivity; the lack of any reliable criterion by which the age of any given specimen can be judged has also proved a serious obstacle. Although a good deal has been ascertained with regard to the breeding habits of the more important species, their seasonal prevalence, their mode of spread from one locality to another, and the manner in which they tide over the cold weather or an unfavourable season, there are many subjects of almost equal importance on which our knowledge is very scanty. Among these might be mentioned the relations of the sexes with reference to copulation and feeding, the length of life and the conditions which determine it, the number of batches of eggs and the time at which each is laid, and the choice of host in the different species. Almost all the observations recorded have been made on female anophelines, and very little is known about the male.

Breeding Habits

As the larvae and pupae of the Anophelina are aquatic and free-swimming, the essential condition for their breeding is a collection of water which will last sufficiently long to enable them to complete their early stages, and which is either stagnant or flows just slowly enough not to wash them away; food material will usually be abundant wherever there is organic matter. Such a condition is to be found almost anywhere, but in addition there are some subsidiary requirements, more or less peculiar to the species, which have to be fulfilled, each species exhibiting a predilection for some particular environment, so that out of the half dozen or so *Anopheles* which may be prevalent in any locality, only two or three will be found in the same breeding place. The choice is more restricted in some species than in others.

A large number of the Anophelina breed in running water, and the larvae of many of the species may be collected from the edges of rivers and streams, where they obtain shelter among dead leaves, sticks and other debris which collects in such places. In small streams which run along dry river beds, and where fresh water collects in pools, larvae can usually be found. Many other species breed in rain water puddles, in rice fields, in irrigation channels, and in wells and tanks. Several species, for instance, *Anopheles ludlowi*, and *Anopheles stephensi*, habitually breed in brackish water, and the latter even in sea water along the coast. *Anopheles costalis*, the commonest West African anopheline, though it usually breeds in water holes and roadside puddles, especially when fouled by the excreta of man and animals, regularly breeds in domestic pots and barrels in native yards in the town of Lagos (Graham). *Anopheles simlensis* and *Anopheles willmori*, on the other hand, prefer to breed in clear mountain streams; *Anopheles turkhudi* is stated by Christophers to breed in river beds in the Punjab, and especially in places where water oozes from sand and where there is much algal growth.

The peculiarity of each species is of practical importance from the point of view of the prevention of mosquito-borne diseases, and the subject has received a due amount of attention. So far as possible the habitat of the larva has been given in the account of the individual species.

Permanent and Temporary Breeding Places

Although the Anophelina do in this way show a certain amount of choice as regards the places in which they deposit their eggs, they will take advantage of any additional collections of water which may come into existence during the rainy season. This is a most important point in the epidemiology of malaria, for it is the occurrence of these temporary but abundant breeding places which renders possible the great seasonal increase in the numbers present in any locality, and the subsequent outbreak of an epidemic.

Bentley in his account of malaria in Bombay, where *Anopheles stephensi* is the incriminated mosquito, draws a useful distinction between the permanent and temporary breeding places. In Bombay its permanent breeding places are the numerous wells, most of which are either actually within the houses or in close proximity to them, and also water cisterns, garden tanks, and similar places; in these situations larvae are to be found in small numbers throughout the year. During and after the rains, however, *stephensi* breeds in surface pools, tubs, buckets, old earthenware vessels, etc., near the houses, and it is to the mosquitoes hatched out in such places that the sudden increase in the prevalence of malaria is to be traced. The explanation of the fact that the larvae are never found in large numbers in the permanent breeding places is that the conditions which have allowed the species to become established in these situations have also permitted of the establishment of their natural enemies, such as predaceous larvae, small fish, etc., while in the temporary breeding places the larvae can grow, and the imagines hatch out, before the natural enemies gain a footing; not only do a larger proportion of the eggs hatch, but most of the larvae attain maturity and become adults. The practical importance of this is evident, for the wells provide a source of supply from which the temporary collections of water, which must inevitably be formed each year, can be stocked with larvae, and unless they are dealt with the appearance of a large number of mosquitoes at the time of the rains will continue.

In the Punjab Christophers has found that the main permanent breeding grounds of *Anopheles* are the large river beds, such as the Jumna and Beas, jheels and large tanks filled with aquatic vegetation, extensive brick fields and excavated tracts, all of which are common around most large towns and even small villages, and lastly the irrigation channels. After the rains temporary breeding grounds are formed by pits and excavations, and shallow accumulations of rain water.

Christophers found numbers of the larvae of *culicifacies* and *fuliginosus* in large sheets of rain water even when there was no obvious food. As this water begins to dry up the larvae are to be found in the deepest holes, and the next shower of rain enables them to complete their development. These extensive collections of water and the resulting deep pools form the most important temporary breeding places for the larvae of *Anopheles* in the Punjab.

Seasonal Prevalence

The seasonal prevalence of mosquitoes depends to a large extent, but not entirely, upon the presence of suitable breeding places. *Stegomyia fasciata*, for instance, occurs all the year round in tropical places with an equable climate; *Culex fatigans* is common throughout the year in Madras, but its numbers are greatly increased in November and December after the rains. A marked seasonal prevalence has been observed among anopheline mosquitoes by workers on malaria in the Punjab. As a general rule all the species are most abundant in the latter half of the year, following on the rains in the early part of July, and diminish as the dry cold weather advances, until there are only a few left in April, when the hot weather commences. The season of the year does not, however, affect the prevalence of all the species in the same way. *A. culicifacies*, for instance, disappears entirely during the cold months of the year, and reappears as the hot weather approaches, although the number of breeding places available by that time is necessarily diminished. James found that in Mian Mir it disappeared about the end of November, to return about the middle of March or the beginning of April; in Ferozpore it is absent from December to May (Adie); at Amritsar it appears in February and March, and is to be found, though in gradually diminishing numbers, up to the onset of the monsoon, after which it becomes exceedingly numerous. *A. fuliginosus*, on the other hand, is distinctly the cold weather species in the Punjab, and continues to lay its eggs throughout the winter; like *culicifacies*, it diminishes in numbers with the advance of the hot weather, but it does not increase in the same way immediately after the rains, the numbers remaining comparatively small until long after *culicifacies* is well established. *A. rossii* disappears entirely in the colder months, and does not reappear till the middle of July. The determining factor is probably the optimum temperature for the development of the larva of each species.

It should be noted that the nature, as distinct from the amount, of the rainfall is important in relation to the prevalence of mosquitoes after the rainy season. Continuous torrential rain tends both to wash away the larvae and to prevent the females from successfully depositing their eggs.

Hibernation and Astivation

Mosquitoes, like all insects which normally have a short life history and which can multiply only under certain conditions, are able to exist, by one means or another, during unfavourable seasons, in order that the race may be carried on. The commonest manner in which this is brought about is by the hibernation of impregnated females, which, finding the season too far advanced to complete the maturation and deposition of their ova, seek out resting places and remain concealed until favourable conditions present themselves at the commencement of the next season. During this period, which may extend to many months in temperate climates such as that of Europe, they feed seldom if at all, and remain in a passive and torpid condition, living upon the store of food material already accumulated, until they are revived by the warm weather. The eggs are then laid, and it is from these first batches of eggs that the mosquitoes of the ensuing season are produced.

Annett and Dutton, in the course of their observations on the hibernation of English mosquitoes, record having found a number of females of *A. maculipennis* in cellars, lumber rooms, wash houses and similar localities in the month of February. In all these situations the anophelines were resting in a *culex*-like attitude; they were difficult to rouse, and when caught in a bottle crawled rather than flew into it. They never found any of the mosquitoes in stables and cattle sheds, as these places were comparatively dry and were constantly warmed by the animals at night. Not a single male *maculipennis* was seen throughout the observations, which extended over several months in the winter; this fact indicates that it is the female alone which hibernates.

Similarly many species 'aestivate' during the hot and dry months in the tropics, when, either from lack of water, or because the high temperature and the dry atmosphere are in themselves unfavourable, the eggs cannot be matured and laid. The adults which survive in this manner are almost, if not quite, all females.

In other cases, and particularly in the tropics, adverse conditions are met by a retardation of the larval stage. The cold weather does not kill off all the larvae, but it inhibits their growth and development, so that this stage may last several months instead of the normal period of a week or ten days. When the weather becomes warmer the larvae again become active and complete their development; the imagines so produced give rise to successive broods with increased rapidity as the weather becomes warmer. It is in this way that *culicifacies* is carried over the cold months of the year in the Punjab.

The eggs themselves, in some species at least, are able to resist unfavourable conditions, such as dryness, for a considerable time; the case of *Stegomyia fasciata* has already been quoted. Cazeneuve records some observations which indicate that they can also resist the action of a very low temperature. He succeeded in hatching out eight *Anopheles* larvae from a block of ice taken from a marsh in North China, where the temperature frequently falls as low as −32° C.

Method of Distribution

The question as to the manner in which mosquitoes spread from their breeding grounds towards the places where they feed is an important one. As a general rule they do not travel far, as they are not structurally adapted for long flights or for travelling in rough weather. At times, however, they are found at a considerable distance from the nearest breeding places, having been either carried there by the wind, or having performed a series of short flights on successive days. One of the writers had experience of the first method of spread in the Aden Hinterland, where, on account of the proximity of infected Arab children and the great prevalence of *Anopheles*, the British and Indian troops were suffering severely from malaria. The camp was moved to another place about a mile from the only breeding ground, the Wady Tiban, but unfortunately it had to be placed on its leeward side. In spite of the distance numerous *Anopheles* could be found in the tents daily, and the conditions were almost as bad as before, although every precaution was taken to prevent larvae being brought into the camp in the drinking water. In this case the mosquitoes were blown across the open country.

James records having found gravid females of *fuliginosus* in Mian Mir at least two and a half miles from the nearest breeding place, and Christophers has noted an instance in which male anophelines have flown at least four hundred yards.

In addition to the direct method of dispersal, anophelines may become distributed over an area indirectly. All the newly hatched imagines of any brood do not necessarily arrive at the same feeding ground as that from which the parent came, nor do mature females necessarily return to the same breeding place on each occasion to deposit their eggs, or return after oviposition to the same house. Starting from any given centre, therefore, breeding places may become established along any radius, provided that suitable collections of water and food supply are available; each of these secondary breeding places may in turn become a centre for dispersal, until eventually the species may be found breeding at a very considerable distance from the place at which it originally occurred. At Mian Mir, for instance, James found that *culicifacies* was able to spread from the surrounding villages into the lines occupied by the British troops by means of isolated houses and breeding grounds between the two. Such breeding places as are of a permanent nature will serve as sources from which surrounding temporary pools may be stocked at the proper season.

In a few cases anophelines are distributed along the ordinary lines of transport, in carts, railway carriages, river boats, and from port to port in ships. Should the conditions at the place at which they arrive be favourable they may become permanently established there.

Larvae of *Anopheles* may be carried long distances down irrigation channels, in which the flow is intermittent, and those which survive may set up new foci. During the anti-malarial operations at Mian Mir the larvae of *culicifacies* were found to be transported in this way into areas from which the imagines were absent.

Age Composition of Anopheles Communities

It has already been stated that we are without any reliable criterion by which the age of a captured anopheline can be judged, or by which the number of batches of eggs which it has laid can be established. Such a criterion would be of great assistance in solving many problems connected with the bionomics of mosquitoes, and in the study of the epidemiology of malaria. The question has been attacked recently by Christophers, and although his preliminary work has not led to any definite conclusions, the subject is of so much importance that an account of it is necessary.

Christophers, after first describing the development of the ova from the early stage up to the time of oviposition, tabulates the process and divides the successive changes into five stages as follows:—

Stage 1. Follicle consists of a group of undifferentiated cells. Follicle and central cells become differentiated.
Follicle cells form a distinct epithelium, like cubical epithelium.
Follicle becomes oval.
Nucleus of the ovum becomes distinguished from those of the nurse cells.
Stage 2. Fine yelk granules appear in protoplasm of ovum.
Coarse yelk granules appear and increase greatly in number.
Ovum increases relatively to nurse cells until it occupies half the follicle.
Stage 3. Nucleus is obscured by yelk.
Ovum occupies ½, ⅔, and ¾ respectively of ovum.
Stage 4. Follicle becomes elongated.
Nurse cells become less and less conspicuous.
Follicle assumes shape of mature egg.
Stage 5. Floats and chitinous structures become visible.
Egg is laid.

Since the second follicle commences to develop before the first is ripe, the ovary is only found in the first stage in the case of a female which is about to develop the first batch of eggs. After laying the first batch the ovary is at the second stage, and thereafter there is nothing to indicate how many batches of eggs have already been matured and deposited. Certain other points are of assistance in determining the age, or rather in separating the very young specimens from the rest. The salivary glands are in an immature stage for the first twelve hours of the life of the imago. The spermathecae nearly always contain sperms beyond the first stage. The mid-gut is practically never free from blood after the first feed except when the ova are nearly ripe, and one may conclude, therefore, that an anopheline without any blood in its mid-gut and with ovaries in the second stage has just laid a batch of eggs, and has not fed since it did so. Occasionally one or two ova are retained while the rest of the batch are deposited, and the presence of these retained ova is proof that the specimen has laid at least one batch of eggs.

From laboratory experiments carried out at Amritsar in July, Christophers found the rate of development to be as follows:—

Twelve hours after hatching ...	Ovaries in first stage, salivary glands immature.
Thirty-six hours after hatching...	First appearance of yelk granules, ovary in second stage.
Fourth day after hatching ...	Ovary in third stage, the nucleus obscured by yelk.
Fifth day after hatching ...	Commencing elongation of follicle.
Sixth day ...	Ovary in fifth stage, appearance of floats.

Observations made on caught anophelines indicated that the rate of development of the second and succeeding batches of eggs is much more rapid than this, and that the second follicle, already at the second stage of development when the first batch of eggs is laid, is able to complete its growth in about two days.

Choice of Host

The nature of the stimulus which induces mosquitoes to bite is not clearly understood. It is well known that mosquitoes, and particularly anophelines, are attracted to dark objects, and seem to prefer to bite through a dark skin rather than a white one. In the Aden Hinterland, in the camp referred to above, the senior writer always found many more *Anopheles* in the tents of Indian soldiers than in those occupied by Europeans; other observers have also noted the same peculiarity in the case of *Anopheles* in Africa. The reason for this choice of host is not very obvious, but it may be noted that the Indians were in the habit of keeping their tents almost completely closed, and the atmosphere in them was much more humid than in those occupied by the Europeans, who kept theirs partly open.

Howletts' experiments tend to throw some light on this subject. This observer carried out a series of preliminary experiments and found that shed blood or human sweat did not attract the females of *Culex fatigans* or *Stegomyia scutellaris* any more than water. On experimenting with the effect of heat, however, it was at once found that the females of *Stegomyia scutellaris* were readily attracted by the hot air radiating from a test tube containing hot water; the male mosquitoes on the contrary paid no attention to it. As a result of a number of similar experiments he concludes that, ‘(*a*) the bite of a mosquito is a reaction to ‘the stimulus provided by a hot surface, (*b*) that the mosquito is attracted ‘to the hot surface mainly by the warm air rising from it, and (*c*) that the ‘strength of the reaction is, within certain limits, proportional to the ‘differential temperature" of the surface, i.e. the difference between its 'temperature and the general air-temperature at the time, and that this 'difference must be positive'.

With our present imperfect knowledge it is not possible to state what other influences may come into play in attracting mosquitoes to bite.

Some Problems in Bionomics

Many interesting problems, some of them of considerable importance, might be stated with regard to the life history and bionomics of mosquitoes in general and the Anophelina in particular. One question is suggested by the well-known fact that female mosquitoes in captivity can be fed and kept alive for some time on a diet of banana, dates, or sugar water. What are the factors which govern their choice of food, and do they only occasionally, or habitually, feed on vegetable juices in addition to blood ? In some regions, as, for instance, certain parts of Greenland, mosquitoes are said to appear in swarms on the advent of a traveller, and to attack him, although previously the region was uninhabited and regular food, at least regular feeds of blood, apparently not available. Are such or any species capable of carrying out their reproductive processes either on a purely vegetable diet or with the aid of the reserve food material carried over from the larval stage, while still retaining the faculty of obtaining and digesting vertebrate blood when the opportunity arises ?

Perhaps the most interesting question, and the one with the most suggestive possibilities, is that of the choice of host from which mosquitoes will suck blood. It is well known that certain species will feed on a variety of vertebrates, though it is by no means certain whether this is pure chance, or whether they are guided in their choice in some definite manner ; * in a considerable proportion of cases the blood parasites of mammals are peculiar to one species, and cannot thrive in the blood of another. If a mosquito, or any other blood-sucking arthropod for the matter of that, takes in from one host the infective stages of a parasite which can normally develop in its body, and at the next feed takes in blood from another host which does not harbour this particular species of parasite, will the blood of the second host affect the progress of the cycle of development of the parasite in its invertebrate host ?

Many other questions will suggest themselves. The above will suffice to indicate the necessity for further enquiry.

Most female mosquitoes may be induced to oviposit in captivity if their eggs are near maturity. When attempting to do this it is best to keep only those females whose ovaries are seen as two white patches at the sides of the abdomen, an indication that the eggs are ready to be laid. Perry also points out that when a number of females are kept together they are much more likely to lay their eggs than if they are kept separately. It is true, however, that the females of some species whose eggs, at the time of capture, do not appear to be mature, will lay them if they are fed and kept long enough.

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* Possibly the difference in the normal temperature of different animals has some influence in the choice of host.

Breeding technique: Egg laying in Captivity

The mosquitoes should be placed either in large test-tubes or wide-mouthed glass jars with screw tops. The method of using the tubes is as follows:—The tube—preferably a large one such as is used for cultivating bacteria on pieces of potato—should be thoroughly cleaned and dried, and a strip of cardboard firmly fixed in it. After the mosquitoes have been placed in it the mouth is covered with a piece of fine-meshed netting; it is then inverted over some moist filter paper in a jar and placed in a dark cupboard. If the mosquitoes are wild ones an attempt should be made to feed them the second night after capture; this is carried out by inverting the tube over the forearm.

The best form of glass jar is the common jam or preserve bottle with a good screw top; these can be purchased in most places at a small cost. The method of using such a jar was first devised by Christophers, and is as follows:—The jar is cleaned and dried, and a strip of cardboard is fixed diagonally across it; it is then inverted over its own screw top, which should contain a very small quantity of water and several strips of filter paper. The mosquitoes, on being placed in the jar, will rest on the cardboard. They can be fed by placing the open end of the jar on the forearm; this is accomplished by raising the jar from its lid until a piece of cardboard can be placed across the mouth; when the jar is in position on the arm the card is withdrawn. In replacing the jar over the lid the cardboard is slipped under its mouth, which is then placed over the lid, and the cardboard gently withdrawn. The tubes and jars should be labelled and placed in a cupboard; in cold weather they should be kept in an incubator which registers a temperature of about 75° F. The tubes and jars should be examined daily to see if any eggs have been laid on the filter paper; all dead mosquitoes and soiled filter paper are removed and if necessary fresh water and paper added. It is best to lift the eggs off the filter paper with a moistened brush, and to place them on a fresh piece of moist paper in a dish containing a small quantity of water; they may, however, be left on the paper in the screw top, care being taken to renew the water.

Collecting Mosquito Eggs

The eggs of mosquitoes may be collected in the places in which they are laid by searching for them with a good hand lens. Those of the Anophelina will be found lying on any vegetable matter at the edge of water, either arranged irregularly or in characteristic star-shaped patterns; their glistening appearance and the presence of floats render them easy of detection. It is often only necessary to collect some of the vegetable matter and to place it in a large tray containing some water, and the larvae will appear in a few days. Small collections of water in tins and pots, in holes in rocks and trees are the kind of places where many Culicines lay their eggs, and it is important to remember that, as in the case of *Stegomyia* and its allies, the eggs may sink to the bottom of the receptacle or hole. In the case of small tins the water should be first stirred up and then poured into a white enamel tray; as a rule the eggs are dark objects and can be readily recognized with the naked eye. In this way many eggs which adhere to the sides of the receptacle are washed out. Small collections of water in holes in trees and rocks are best removed by syphoning off the water after stirring it up; if it is thought that any of the eggs are adhering to the sides of the hole fresh water may be added, and the process repeated until they have all been recovered. The well-known egg rafts of many Culicines are such large objects that they cannot escape detection; they are best lifted out of the water with a brush.

When the larvae hatch out of the eggs thus collected they should be transferred to specially constructed breeding trays or tanks. The important points connected with the rearing of mosquito larvae are dealt with below.

Collecting Mosquito Larvae

Large numbers of mosquito larvae may be collected by dipping for them at the edges of streams, ponds, tanks and similar places. The simplest form of dipper, and one with which large numbers of larvae can be captured in a short time, is a shallow white basin, of which several sizes may be used. One side of the basin is lowered towards the surface of the water where the larvae are floating, and with a sudden movement its edge is passed under the water, which as it flows in carries the larvae with it. The water containing the larvae is then poured into a large bucket, and the dipping process repeated as often as is desired. Large spoons are also used for collecting larvae, but only a few can be caught with them at each dip. In large pools where there is a quantity of thick vegetation it is often difficult to locate the larvae, for they shelter themselves among the stems and leaves of the water plants and can only be captured one at a time. In this case it is best to pull out most of the plants and, when the larvae have collected together after an interval, to dip for them in the usual way.

Larvae may be collected from wells by using a simple and efficient form of apparatus devised by Bentley, the construction and use of which he describes as follows :—'A loop about fifteen to eighteen inches in diameter 'is made of very thick brass or galvanized iron wire, and upon this frame 'a shallow net of very thin mull-mull or muslin is stretched. The net is 'suspended by three short brass chains about two feet long, which are 'attached to the frame below and to a small ring above. To the ring 'a rope is tied, and the net can be lowered to any required depth. When 'a well has to be examined the net is lowered to about a foot beneath the 'surface of the water, the weight of the frame causing it to sink. It is 'gently moved below the surface, and pulled up at a point some distance 'from where it first entered the water. On examining the net, larvae, 'if plentiful, are easily seen and can be secured by washing them off into 'a bowl of clean water'. Bentley also recommends washing the net in a large-sized white enamel frying pan.

Identification of larvae

In the laboratory the different kinds of larvae should be separated out, care being taken that predaceous species, such as those of *Culex concolor*, and dragon fly larvae, are removed to separate trays. The more important characters of taxonomic value, such as the structure of the antenna and syphon tube, the position of the palmate hairs and the number and structure of the leaflets, can be studied in the living larva; for finer details it is best to make cleared preparations. With a little practice the worker will learn to recognize the larvae of the various species which are present in his neighbourhood. The several species of mosquito larvae which may be found breeding in the same collection are best identified by transferring them singly, with the aid either of a glass pipette or a small spoon, to a slide and placing a coverslip over them. In this way they are immobilized, though in no way damaged, and can be examined with a low power objective; in the case of larger larvae it may be necessary to place them in a hollow glass slide.

If a few imagines are required merely for purposes of identification larva may be kept in small trays, but it will soon be found that they do not thrive in these receptacles. It is difficult to obtain water containing suitable food and to keep it fresh.

In order to obtain the best results in rearing mosquito larvae they should be placed in some form of breeding tank; the trays used in the case of tabanid larvae (see Chapter 4, Section 2) will be found very useful for this purpose. The tray should be filled with a layer of sand and mud to a depth of three or four inches, and the mud sloped off to simulate the edge of a pond; fresh water is then poured into the tray until it is about three-quarters full. Some plants and grass should be dug out with their roots from the edge of a pond and planted in the mud; not only do they afford excellent shelter for the larvae, but their stems and leaves harbour animalculae and other forms of animal life suitable for food. The tray should be placed in front of a window or on a verandah with an eastern position, so that it receives direct sunlight for several hours in the morning. It may be necessary to cover the tray with a net in order to prevent stray mosquitoes from laying their eggs in the water; this is accomplished by fixing stout wires to the sides of the tray, as is described in the case of the breeding of the Tabanidae. If large numbers of adult mosquitoes are required for feeding experiments, larvae can be added to the tray daily, so that imagines will be available on each successive day.

Raising of imagines from larvae

In the case of tabanid larvae, at least those of the larger species, little or no attention need be paid to the condition of the water in the tray; although it may become stale, the larvae do not suffer much in consequence. With mosquito larvae, however, it is very different. After the water has been standing for several days a pellicle, consisting of flagellates, amoebae and bacteria, forms on the surface, and below this decomposition takes place. This has a most injurious effect on mosquito larvae, and if it is not attended to they cease to grow and eventually die. It is, therefore, important to aerate the water morning and evening, by forcing air through it; a fine capillary tube and a rubber bulb, such as that attached to some form of syringe, may be used. Darling recommends the well-known Pacquelin cautery apparatus, which is used by attaching the double bulb to a glass tube with a capillary canal; the air is forced through the glass into the water, which then remains fresh for a long time.

Methods of keeping and feeding mosquitoes

When the larvae pupate, the pupae should be collected with a small spoon and transferred a small jar, which is three-quarters full of water. A similar jar, with a piece of cardboard fixed inside it, is inverted over the mouth of the first; both should be kept in a safe place. When the mosquitoes hatch out they fly into the upper jar and rest on the cardboard; when all the imagines have hatched the upper jar should be removed and a piece of netting tied over its mouth.

Darling recommends keeping mosquitoes in lantern chimneys, in the centre of which he fixes a circular piece of cardboard, securing the two ends with pieces of net; about twenty mosquitoes are placed in each chimney, which should be placed in a jar with some moist filter paper and kept in a cupboard.

Adie describes a simple method of keeping anophelines alive without feeding them on blood. In the jar he places a dried date wrapped in a small piece of muslin, a piece of wet sponge, and a twig of some green weed, the end of which is inserted into a hole in the sponge. If placed in a jar or lamp chimney under these conditions female anophelines may be kept alive for three weeks without blood.

Caught mosquitoes can be induced to bite if certain precautions are attended to. The worker will, however, soon discover that many if not all of the *bred* females of certain species will refuse to suck blood; no adequate explanation can be given for this, but it seems probable that copulation is in some way connected with the first feed of blood. Although female mosquitoes will readily suck the juice from a banana or a date, it has been shown that this food has no material effect on the development of the ova. It is clear, however, that a preliminary feed from a banana or a date will stimulate mosquitoes to bite later on.

Feeding experiments should preferably be carried out in the evening, and at least twenty-four hours after the mosquitoes have hatched. The jar or the chimney should be inverted over the patient's forearm, and care should be taken to cover it with a dark cloth in order to exclude all light. A few taps on the bottom of the jar will cause the mosquitoes to alter their position, and if they are going to bite they will settle on the net and commence to feed at once; in the case of the lamp chimney the same effect is produced by blowing through one end. After the mosquitoes have fed the jar is inverted over its lid, which should contain some moist filter paper. The chimneys should be placed upright in a jar, at the bottom of which there is some moist filter paper.

If the mosquitoes refuse to bite an attempt should be made on the following night, and in the interval they should be given a date or raisin to feed on. If they still refuse to bite they should be liberated into a large cage covered a good net; the bare arm should be passed inside the cage in the evening first moistening it with a little water. Sometimes even this method fails, and if this happens the mosquitoes should be liberated into a net fitted over a patient's bed. One of the writers found that this was the only way to feed *Culex fatigans*, which had been hatched from eggs, on Kala Azar patients. This last method of feeding mosquitoes is, however, seldom necessary.

Mosquitoes can be fed on small birds, such as sparrows, canaries, owls, and pigeons, by liberating them in large cages containing the birds. Several strong wire supports should be fixed inside the cage for the birds to rest on. A muslin bag is secured over the head of the bird by tying it securely with two tapes under the wings; this prevents it from flying about in the cage.

Pitfalls in feeding experiments

In all feeding experiments with mosquitoes which have for their object the investigation of the life history of some protozoon it is imperative to use bred insects. It has already been pointed out that the early stages of certain flagellates of the genera *Herpetononas* and *Crithidia* occur in the alimentary tracts of mosquito larvae, so that breeding out the adults from larvae is not a certain means of excluding these parasites; spirochaetes and certain microsporidia are also acquired by mosquitoes early in their larval stages. In the past these parasites have been a fruitful source of error, and there can be no doubt that they have been confused with blood parasites which the mosquitoes may ingest. The only way to exclude such parasites is to breed out the imagines from eggs, and to take the precaution of keeping the larvae in water which does not contain any encysted stages. The possibility of heriditary transmission should not be forgotten.

The methods employed in dissecting mosquitoes will be dealt with at the end of Chapter IV.

CHAPTER III

SECTION 2

THE ORDER DIPTERA: ORTHORRAPHA-BRACHYCERA

THE characteristic feature of this division of the Orthorrapha is the short type of antenna. Usually there are two or three simple joints, with or without a terminal arista, which in itself may consist of one or two joints with a terminal style. There is, however, a good deal of variation in the form of the antenna in the different families. In the Phoridae, for instance, the antenna consists of two or three simple joints, with a dorsally placed arista, thus approximating to the type seen in the Muscoidean flies, while in the Asilidae there are three joints and a terminal style. In the Tabanidae the antenna is specially modified and of an unusual shape. The wing venation is always more complex than that in the nematocerous flies; a discal cell is always present, and the second long vein is never forked.

Of the families contained in this division the Tabanidae are by far the most important, both because of their numerical preponderance and of the occurrence of the blood-sucking habit in so large a proportion of the species. In the Leptidae there are three or four species which are said to suck blood, but the habit is the exception rather than the rule in that family. The Asilidae, or 'robber flies', are well known predaceous insects; certain African species are said to attack man occasionally, though it is doubtful whether they do so with the intent to suck blood.

FAMILY TABANIDAE

Large, small, or medium-sized flies, with robust thick-set bodies and large heads, the surface of which is almost entirely occupied by the compound eyes. Antennae porrect and variable in structure, and always three-jointed; the third joint is composed of from four to eight segments more or less distinctly separated from one another. In most of the genera the antennae are shorter than the head; in Chrysops they are longer. The third joint often ends in a short or long blunt-pointed process. The eyes may be pubescent or bare, contiguous or nearly so in the male, with variously coloured bands in which the facets are large; in the female the *eyes are separated by a broad white band, at the lowest border of which there are certain small dark longitudinal or transverse callosities or calli. Ocelli may be present or absent. Proboscis short or projecting downwards, or long and projecting forwards. Palpi two-jointed, stout, of a pale creamy colour, as long as the proboscis or much shorter. Thorax broad, covered with fine hairs, never with bristles, and with or without stripes or other markings. Abdomen broad, composed of seven visible segments, and covered with delicate hairs, never with bristles; it may be marked with spots and bands. Male genitalia never prominent. Legs stout, tibiae sometimes dilated, middle tibia with two spurs at the tip. Empodium well developed, pulvilli always present. Venation characteristic and without much variation; two submarginal and five posterior cells present. The costal vein encircles the entire wing; the anterior branch of the third longitudinal vein often has a short backwardly directed spur. Wings often dark, with interrupted bands, clear flecks or rings. Squamae of large size. Reproduction oviparous, eggs laid in a mass on leaves or twigs over or near water. Larvae whitish, cylindrical in shape and tapering at both ends; they may be ringed or striped, and are provided with pseudopods and rows of small spines for locomotion. The pupa resembles that of Lepidoptera, but has large ear-shaped spiracles on the dorsum of the thorax.*

This family is an extremely large one, no less than 2,500 species having been recorded up to the present time. It is widely distributed, and many of the species are common in favourable localities. The males throughout the family, and the females in many of the genera, are flower feeders or live upon vegetable juices. In some of the genera, such as *Tabanus*, *Haematopota* and *Chrysops* the females are blood-suckers, and the commoner species, which are brought to notice by their habits, have received various local names, such as 'gad flies', 'horse flies', 'clegs', 'seroot flies'. They feed mainly upon cattle and horses, but will occasionally attack man. The males of many of the species are very rarely met with, even in localities in which the females are quite common.

Several observers have attempted to incriminate flies of this family as transmitting agents in certain trypanosome diseases of equines and camels, such as Surra and Debab, in India and North Africa. The evidence in the majority of instances is circumstantial, and is not borne out by transmission experiments. It is possible that the Tabanidae may transmit the trypanosomes accidentally. (See Chapter XII.)

Classification and Identification

Although it is generally easy enough to allocate a specimen of one of the commoner genera, such as *Tabanus*, *Haematopota*, or *Chrysops*, to its proper genus, the identification of species in this family is often extremely difficult. The characters to be particularly noted are the size and shape of the frontal callus, and the character of its backward extension; the shape and breadth of the front; the structure and shape of the palpi and antennae, and especially of the terminal joint of the latter. Mere examination of the antenna with a hand lens is apt to be misleading, as one frequently finds it very difficult to determine the exact number of the joints or rings, and their relative size, in this manner; it is advisable to remove the part and to clear it in potash solution, and then to mount it in canada balsam for examination under the microscope. The colouration and banding of the eyes, which is often extremely characteristic, especially in the male, is not to be depended on as a taxonomic character, as it fades rapidly after the death of the insect. It should be noted in the fresh condition and recorded.

Among the authorities on this family may be mentioned Austen, Grünberg, Newstead, Ricardo and Sourcouf, in Europe; Hine and Williston in North America; Lutz and Nieva in South America. Hine's papers on the life histories and breeding of the American species are of special practical value.

The following key, to which some additions have been made, is taken from Miss Ricardo's papers:—

FAMILY TABANIDAE

A.	Hind tibiae with spurs; ocelli usually present	Subfamily **Pangoninae.**
B.	Hind tibiae without spurs; ocelli absent	Subfamily **Tabaninae.**

A

SUBFAMILY PANGONINAE

1.	Third joint of antenna with eight or at least seven segments; proboscis usually prolonged		2
	Third joint of antenna with five segments; proboscis short	**Silvius, etc.**	12
2.	Third joint of antenna with a tooth	**Dicrania.**	
	Third joint of antenna without a tooth		3
3.	Wings short; body short and elliptical	**Apocampta.**	
	Wings short		4

4.	Third joint of antenna with each segment branched	**Pityocera.**
	Third joint of antenna not branched	5
5.	Upper corner of eyes terminating in an acute angle	**Goniops.**
	Upper corner of eyes not terminating in an acute angle	6
6.	Antenna deep-seated, inclined downwards; palp very large and thick	**Cadicera.**
	Antenna not deep seated not inclined downwards; palp not very large and thick	7
7.	Antenna subulated; proboscis with terminal lips in form of a hatchet; anal cell open and anal vein curved	**Pelecorhynchus.**
	Antenna not subulated; proboscis simple; anal cell closed, anal vein not curved	8
8.	Proboscis scarcely extending beyond palpi	**Apatolestes.**
	Proboscis extending beyond palpi	9
9.	Wing with fourth posterior cell closed	10
	Wing with fourth posterior cell open	11
10.	Eyes not bare	***Scione.***
	Eyes bare	**Dorcalaemus.**
11.	Wing with first posterior cell closed; eyes bare or hairy (including subgenera	**Pangonia.** **Erephrosis** and **Subpangonia.**)
	Wing with first posterior cell open; eyes hairy or bare (including subgenus)	**Diatomineura.** **Corizoneura.**

SILVIUS AND ALLIED GENERA

12.	First and second joints of antenna short	13
	First and second joints of antenna long	18
13.	First joint of palp thickened	***Scepsis.***
	First joint of palp not thickened	**Adersia.**
14.	Second segment of abdomen unusually large; spurs on tibiae small	**Pronopes.**
	Second segment of abdomen not unusually large; spurs on tibiae not unusually small	15
15.	Face concave in the middle	**Rhinomyza.**
	Face not concave in the middle	16
16.	Wings with first posterior cell open (including subgenus	***Silvius.*** **Esenbeckia.**)
	Wings with first posterior cell closed; frontal callus absent	**Aegophagamyia.**
	Wings with first posterior cell closed; frontal callus present.	**Bouvierella.**
17.	Third joint of antenna with an acute spine on the first annulation	**Gastrixodes.**
	Third joint of antenna with no spine on the first annulation.	18
18.	Second joint of antenna as long, or nearly as long, as the first joint; wings usually with black or brown designs	**Chrysops.**

B

SUBFAMILY TABANINAE

1.	Third joint of antenna consisting of four divisions, without a tooth or angulation	2
	Third joint of antenna with five divisions	5

2.	Rings of the third antennal joint so distinctly divided that the antenna appears as if six-jointed	**Hexatoma.**
	Rings of third antennal joint not so distinctly divided; the antenna always appears as if three jointed	**3**
3.	Wings marked with rings and circles of darker colouring	**Haematopota.**
	Wings not so marked	**4**
	Wings dark with light markings, but without the characteristic streaks of *Haematopota*	**Hippocentrum.**
4.	First and second antennal joint in the male pubescent; third joint longer than the first. Eyes hairy	**Dasybasis.**
5.	First antennal joint globular situated on a protuberant projection of the forehead	**Boldodimyia.**
	First joint of antenna not globular	**6**
6.	Third joint of antenna simple, not furnished with a tooth or angular projection	**7**
	Third joint of antenna furnished with a tooth or distinct angular projection	**9**
7.	Body covered with metallic scales	**Lepidoselaga.**
	Body metallic in colouring	**Selasoma.**
	Body without metallic scales or colouring; the first antennal joint longer than is usual in *Tabanus*; wings usually with brown markings	**8**
8.	Antenna long, the third joint cylindrical and situated on a projecting tubercle	**Udenocera.**
	Antenna short, *Tabanus*-like, situated on a prominent tubercle	**Neotabanus.**
	Antenna not very long, the third joint not cylindrical, and not situated on a projecting tubercle	**Diachlorus.**
9.	Abdomen short, stout and very convex	**Stibasoma.**
	Abdomen neither short, stout or convex	**10**
10.	Antenna long and slender, the first joint long	**Acanthocera.**
	Antenna neither long or slender, nor is the first joint long	**11**
11.	Species of a slender build, usually with a banded thorax and abdomen; third joint of antenna slender, mostly with brown markings on wings	**Dichelacera.**
	Species of a stouter build; third joint of antenna stout	**Tabanus.** (sens. lat.)

In the above key three Ethiopian genera, *Thaumastocera*, *Holoceria* and *Parahaematopota*, recently erected by Grünberg, have been omitted, as each contains only one species. According to Grünberg the genus *Thaumastocera* (*T. akwa*, Grün.) is separated from the South American genus *Stibasoma* by the curiously shaped third segment of the antenna, which has two deep notches in its superior margin in the female; in both sexes the angle at the base (superior) is extended into a process which extends as far as the end of the joint. *Holoceria* (*H. nobilis*, Grün.) and *Parhaematopota* are closely allied to *Haematopota*, and are considered by Austen to be of doubtful validity. *H. nobilis* has the general facies of a *Haematopota*, but is without the characteristic streaks and circles of white on the wings. The thorax is dark, with two admedian dark bands; abdomen of a steely grey. According to Neave it is widely distributed in the wooded parts of eastern tropical Africa.

Hine gives the following Key to the North American genera of Tabanidae:—

1. Hind tibiae with spurs at the tip 2
Hind tibiae without spurs 6
2. Third segment of the antenna composed of eight annuli the first of which is only a little longer than the following ones 3
Third segment of the antenna composed of only five annuli the first of which is much longer than the following ones; ocelli present 5
3. Front of male narrow; ocelli present or absent; fourth posterior cell at least open . . . . **Pangonia.**
(Diatomineura, Corizoneura.)
Front of female broad with a denuded callus; ocelli present 4
4. Eyes in the female acutely angulated above; wing in both sexes with a dark picture . . . . **Goniops.**
Eyes in the female not acutely angulated above; wings hyaline. . . . . **Apatolestes.**
5. Second segment of the antenna about half as long as the first; eyes in life with numerous small dots . . . . . **Silvius.**
Second segment of the antenna as long or but little shorter than the first; wing with a dark picture . . . . **Chrysops.**
6. Third segment of the antenna with a well developed basal process . . . . **Tabanus.**
(Therioplectes, Atylotus.)
Third segment of the antenna without, or with a rudimentary basal process 7
7. All the tibiae enlarged, the hind pair ciliate . . . . **Snowiellus.**
None of the tibiae enlarged and the hind pair not ciliate. 8
8. Front of the female as broad as long; the callus transverse . **Hematopota.**
Front of the female narrow . . . . **Diachlorus.**

GENUS TABANUS, L.

Small to very large thick-set insects. The head is as a rule broader than it is high; the eyes may be nude or hairy. In the male the eyes have irridescent bands, in which the facets are larger than in the rest of the surface. The colours of these bands fade rapidly on the death of the insect. In the female there are no irridescent bands and the colouration is usually uniform; in some species the females have brightly coloured bands, in which case the eyes of the male are similarly marked on the lower surface. In a few species (subgenus Therioplectes, Zeller) the eyes are pubescent, but the hairs as a rule are not very apparent. Ocelli are always absent, but there may be a small tubercle on the vertex (Therioplectes); it is absent in the subgenus Atylotus. The eyes of the female are widely separated; situated on the forehead between them there are *usually one or two small raised knobs or bands of a dark colour, the calli; the lower of these may be transverse or broadened transversely, the upper round or oblong; in the majority of species one of these is produced upwards to the vertex as a narrow line; rarely both are so produced. One or both of the calli may be absent. The antennae are three-jointed and are shorter than the head; the proximal joint is short, the second very short, only about one-third as long as the first, the distal joint as long as the first and second together. The third joint is styliform, consisting of four segments, and has a dorsal spine or hook at its basal end. The thorax is broad, and often has longitudinal stripes. The abdomen is slightly broader than the thorax, and may be banded with stripes or only marked with spots. The wings are large, and usually clear, but there may be spots and bands. The anterior branch of the third longitudinal vein may or may not have a backwardly directed spur.*

Miss Ricardo gives the following table of the Oriental species of Tabanus:—

TABLE OF GROUPS

I.	Eyes bare	II
	Eyes hairy (*Therioplectes*)	GROUP XI
II.	Forehead with two separate calli, the first one usually transverse, the second irregular in shape, smaller. Forehead four to six times as long as it is broad. Small species 9 to 14 mm. in length	III
III.	Thorax and scutellum same colour. Abdomen with no bands	GROUP I
	Scutellum white or yellow-haired. Abdomen with white or yellow-haired bands	GROUP II
IV.	Forehead with two small round spot-like calli, one above the other, never united	GROUP III
V.	Forehead with no callus	GROUP IV
VI.	Forehead with one square, narrow, or oblong callus, which is always prolonged towards the vertex by a more or less narrow line	VII
VII.	Wings with spots or bands	GROUP V
	Wings distinctly marked with brown or yellow colouring, but not in the form of bands. Large species 18 to 23 mm. in length	GROUP VI
	Species with one or more stripes, usually continuous, on abdomen. Forehead five to nine times as long as it is broad	GROUP VII
	Species with median or lateral spots or both on abdomen, not usually forming a continuous stripe. Forehead four to ten times as long as it is broad	GROUP VIII

Species with paler bands and sometimes spots on abdomen. Forehead four to ten times as long as it is broad . . . Group IX

Species with abdomen unicolorous or almost so, sometimes darker at apex. Forehead five to ten times as long as it is broad . . . Group X

VIII. Species with eyes pubescent and an ocelligerous tubercle on forehead at vertex . . . Group XI

Table of Species

Group I.

1. Subcallus shining. Eyes with no cross-bands . . . 2
   Subcallus not shining. Eyes with cross-bands . . . 3
2. Frontal callus reaching eyes. Abdomen grey, covered, with long white pubescence. Tibiae whitish, with long fringes of white hairs . . . **rarus.** (Federated Malay States.)
   Frontal callus not reaching eyes. Abdomen black, shining. Tibiae whitish, but with no long fringes of white . . . **hirtipalpis.** (Nepal.)
3. Frontal callus reaching eyes. Black species with three grey stripes on abdomen . . . **bicallosus.** (Pusa, Bengal; Madras.)

Group II.

4. Dark brown or yellowish-brown species with yellow-haired scutellum and yellow-haired bands on abdomen . . . 5
   Black species with white-haired scutellum and white-haired bands on abdomen . . . 6
5. Abdomen reddish brown or yellow with six narrow yellow bands. Palpi pale yellow with black and yellow pubescence. Fore tibiae pale on basal two-thirds only . . . **flavicinctus.** (Assam; South India.)
   Abdomen dark reddish-brown or blackish with two broad yellow bands. Palpi black with grey tomentum, and white and black hairs. Fore tibiae pale to apices . . . **leucocnematus.** (Assam, Burma.)
6. Abdomen black with two white bands. Frontal callus almost reaching eyes. Fore tibiae pale on basal two-thirds only. Wings tinged brown on fore border . . . **bicinctus.** (South India; F. Malay States.)
   Abdomen with six white bands. Frontal callus not reaching eyes. Fore tibiae pale to apices. Wings clear . . . **sexcinctus.** (Burma.)

Group III.

7. Forehead slightly narrower anteriorly, three and a half to four times as long as it is broad . . . 8
8. Abdomen blackish covered with golden yellow tomentum and appressed yellow pubescence . . . **fulvus.** (China.)

Abdomen yellowish with median and lateral blackish or brownish stripes . . . **ditaeniatus.**
(Africa to India; China and Japan; common in South India.)

Group IV.

9. Abdomen brown, reddish at base, covered with grey tomentum and with two small round greyish spots on the segments. Wings with no appendix. Length 7½ to 11 mm . . . **virgo.**
(Bengal; South India.)

Abdomen blackish brown with median and lateral greyish tomentose spots. Wings with an appendix. Length 13 mm. **nemocallosus.**
(Bengal.)

Abdomen covered with greyish-yellow tomentum and with thick short yellow pubescence in female; abdomen of male the same but a black median stripe often appears. Wings with no appendix. Length 11½ to 12½ mm. . . . **negativus.**
(Formosa; China.)

Group V.

10. Wings with four dark spots. Abdomen reddish brown, with white spots . . . **javanus.**
(Java.)

Wings with one cross-band, the first posterior cell open . . . 11
Wings with two cross-bands, the first posterior cell closed or very narrow . . . 12

11. Forehead narrowest at vertex. Abdomen reddish, darker at apex, with small white median spots . . . **optatus.**
(Bengal; Borneo; Sumatra.)

Forehead narrowest anteriorly. Abdomen yellowish, darker at apex with larger white spots . . . **non-optatus.**
(Bengal.)

12. Abdomen brownish yellow, with broad yellow posterior bands on each segment, under side yellowish. Antennae reddish yellow. Male with equal facets to eyes . . . **flexilis.**
(Celebes.)

Abdomen brownish red with narrower yellow bands, under side darker. Antennae reddish yellow, black at apex. Male with unequal facets to eyes . . . **vanderwulpi.**
(Philippines.)

Group VI.

13. Wings dark rich brown, the disal cell clear. Large black species with orange red pubescence on face and breast. Antennae red . . . **pratti.**
(Malacca; Sarawak; Selangor.)

Smaller species similar in colouring. Antennae black . . . **fuscicornis.**
(Formosa.)

Wings yellowish or brownish, very distinctly tinged with brown at apex and on posterior border. Scutellum yellow or greyish . . . 14

14. First posterior cell of wings closed or very narrow . . . 15
First posterior cell open, not very narrow . . . 16

15. Abdomen reddish brown, narrow, with grey tomentose bands and median spots. Palpi slender. First posterior cell closed . . . . **nephodes.** (Assam.)

Abdomen brown with narrow grey tomentose bands but no median spots. Palpi, large, broad. The first posterior cell very narrow at border . . . . **albofasciatus.** (Assam.)

Abdomen black, livid at base. Smaller species. First posterior cell closed . . . . **basalis.** (Sumatra.)

16. Large yellowish species with blackish bands on the abdomen . **auriflamma.** (Sylhet, Assam.)

Group VII.

17. First posterior cell closed. Yellowish species with indistinct median black stripe on abdomen . . . . **annamitus.** (Male) (Cochin China.)

First posterior cell open 18

18. Frontal callus oblong or narrow with lineal extension. Forehead at least five times as long as it is broad 19

Frontal callus large, somewhat protuberant, almost square, with short lineal extension. Forehead three or four times as long as it is broad 36

19. Abdomen with a median stripe and lateral stripes or spots 20

Abdomen with one median continuous stripe only, no lateral spots, or only isolated ones on the second segment 27

Abdomen with lateral stripes only 35

20. Frontal callus with a spindle-shaped lineal extension 21

Frontal callus with the lineal extension not spindle-shaped 22

21. Abdomen blackish or reddish brown with grey median and lateral stripes, almost all the same length . . . . . **striatus.** (Widely distributed throughout India; Burma; Assam; Ceylon; Malay; Sumatra; Java and Philippine Islands.)

Abdomen with grey median stripe beginning only on the third segment, and with lateral stripes ending on the third or fourth segment . . . . **hilaris.** (Bengal; Assam; S. India.)

22. Abdomen with a median stripe, the side spots small and indistinct 23

Abdomen with a median stripe, the side spots large and distinct. 24

23. Smaller species. Abdomen reddish yellow, darker at apex. Thorax blackish. Forehead eight times as long as it is broad . . . . **abbreviatus.** (Bengal; Java; Formosa.)

24. The median abdominal stripe composed of almost equal sized spots not very large 25

The median abdominal stripe composed of spots of unequal size, those on the third and fourth segments very large and conspicuous 26

25. Abdomen and thorax lilac or blackish brown, femora blackish. Forehead about five times as long as it broad . . . **rubidus.**
(Bengal; Bombay; Assam; South India; Malay Peninsula; Java; Sumatra; closely allied to **autumnalis** and **albimedius.**

Abdomen and thorax obscurely reddish brown, femora reddish brown. Forehead five to six times as long as it is broad .. **albimedius.**
(Widely distributed in India; Nepal to Ceylon; Bombay to Bengal.)

26. Abdomen and thorax reddish brown, femora blackish. Forehead about seven times as long as it is broad . . . **speciosus.**
(South India; Ceylon.)

27. Median stripe of abdomen grey tomentose, or white or yellow-haired **28**
Median stripe of abdomen black **31**
Median stripe of abdomen golden haired **32**

28. Forehead barely half as wide anteriorly as it is at vertex. **29**
Forehead parallel or nearly so **30**

29. Small brown species. Femora brownish. Wings clear, brown on fore border . . . . . **hirtistriatus.**
(Federated Malay States.)

30. Large black or reddish brown species, median abdominal stripe narrow. Femora black. Wings tinged brown . . **monotaeniatus.**
(Assam.)

Brown species, the median abdominal stripe broad, the two round spots on second segment. Femora reddish wings brown on fore border . . . . . **brunnipennis.**
(Siam; United Provinces; India.)

31. Abdomen reddish, black at apex, a narrow grey stripe often apparent on the median black stripe . . . . . **abscondens.**
(Burma.)

32. Forehead parallel **33**
Forehead narrower anteriorly **34**

33. Abdomen yellowish brown, darker at apex, the median stripe a dull, golden hair indistinct . . . . . **auristriatus.**
(Canara, India)

34. Abdomen yellowish brown or dark brown, the median stripe broad. Fore femora yellowish. Wings brown, especially on fore border . . . . . **hybridus.**
(Assam; Malay; Sarawak; Borneo; South China.)

Abdomen covered with yellowish tomentum, median stripe very broad. Fore femora black. Wings clear . . . **aurotestaceus.**
(China.)

35. Black species. Abdomen with ferruginous lateral stripes on the first four segments. Legs blackish brown . . **tristus.**
(Sumatra.)

36. Forehead narrowest anteriorly **37**
Forehead narrowest at vertex **38**

37. Small black species. Abdomen with a median grey stripe beginning on the third segment only, the lateral stripes terminate on the second segment . . . . . **jucundus.**
(Punjab; N.-W. Provinces; Bombay; Ceylon; China.)

38. Small brown species. Abdomen with a median grey stripe . **puteus.**
(Ceylon.)

Group VIII.

39. Wings with first posterior cell closed or at least very much narrower at border. Forehead six to seven times as long as it is broad **40**

Wings with first posterior cell open, never very narrow at border **41**

40. Abdomen with three series of grey spots on abdomen, reddish brown in male, blackish in female . . . . . . **amaenus.**
(China; Formosa; Japan.)

Abdomen with three grey spots on the first two or three segments only, a larger, broader bodied, blackish species . **mandarinus.**
(China; Formosa; Japan.)

41. Forehead narrow, six to ten times as long as it is wide anteriorly, with a long narrow frontal callus **42**

Forehead broader, four to five times as long as it is wide anteriorly, with a larger nearly square, or pear-shaped frontal callus **52**

42. Brown, reddish brown, or reddish yellow, medium sized or large species, the triangular greyish or yellowish spots not usually forming a continuous stripe **43**

Large unicolourous reddish species with small median indistinct white spots **49**

Reddish brown or brown species with large prominent median whitish spots on the third and fourth segments only **50**

Reddish species with black spots **51**

Small species with a narrow yellow abdomen irregularly marked with black and with three series irregular shaped grey median and lateral spots . . . . **varicolor.**
(Borneo.)

43. Medium sized species, 17 to 18 mm. in length. Abdomen reddish yellow with small median white spots. Forehead almost parallel or barely a third narrower anteriorly, six times as long as it is broad. Frontal callus oblong, not reaching the eyes. Wings clear, faintly tinged yellowish brown . . . . **rubicundus.**
(Assam.)

Large brown or reddish brown species usually 18 to 25 mm. in length with abdominal median spots. Forehead from one-third to half narrower anteriorly, frontal callus long and narrow **44**

44. Forehead eight to nine times as long as it is broad, about one-third narrower anteriorly **45**

Forehead very narrow, eight to ten times as long as it is broad, only half as wide anteriorly as at vertex **46**

45. Abdomen reddish, or reddish yellow, large, broad, with median short triangular yellow spots often indistinct. Fore tibiae reddish yellow on basal half, with black pubescence. Wings large, tinged yellowish brown or almost clear. Forehead almost parallel . . . . **stantoni.**
(Malay.)

Abdomen reddish brown, long, narrow, with median long triangular, distinct whitish spots, usually joining each other. Fore tibiae white on basal half with white pubescence. Wings long, faintly tinged yellowish brown. Forehead about a third narrower anteriorly . . . . . . **indianus.**
(Canara, S-W. India; Formosa.)

Abdomen blackish brown with almost hemispherical white medium spots. Fore tibiae blackish. Legs and palpi blackish. Wings clear, tinged brown. Forehead about a third narrower anteriorly . . . . **brunneus.**
(Java.)

46. Forehead eight times longer than it is broad, the frontal callus not reaching eyes **47**

Forehead ten times as long as it is broad, the frontal callus reaching eyes **48**

47. Abdomen dark reddish brown or reddish yellow, with indistinct small greyish or yellow-haired median spots often absent. Thorax blackish with some yellowish grey tomentum. Fore tibiae pale on basal half. Wings slightly tinged with brown. Male with unequal facets on eyes . **fumifer.**
(Malay; Sumatra; Borneo.)

Smaller species. Abdomen reddish brown with distinct bright yellow haired median spots, and similar lateral spots on the second to fifth segments. Thorax blackish with greyish yellow tomentum . . . . **malayensis.**
(Malay.)

Larger species. Abdomen broad, reddish brown with indistinct median spots and some lighter segmentations. Thorax reddish with some grey tomentum. Wings nearly clear. Fore tibiae pale on basal two-thirds. Male with equal facets to eyes . . . . **factiosus.**
(Celebes; Philippines.)

48. Abdomen reddish brown, median spots indistinct, small whitish. Thorax reddish, thickly covered with ashy grey tomentum. Wings clear . . . . **dissimilis.**
(Borneo.)

49. Abdomen and thorax reddish, shining, nearly devoid of pubescence. Wings clear. Palpi ending in an acute point . **ignobilis**
(Borneo.)

Abdomen and thorax reddish, Wings tinged yellowish brown, Palpi ending in an obtuse point . . . . **nexus**
(Borneo.)

50. Red-brown species with the large median white spots on third and fourth segments of abdomen, and white spots on the lateral borders of first four segments. Tibiae reddish (Male) . . . . **signifer.**
(China.)

Brown species with the same median spots, but with lateral white spots on the first two segments only. Tibiae white . **significans**
(India; Federated Malay States.)

51. Abdomen reddish, the apex dull black with large black median spots on the second and third segments . . . . **fuscomaculatus**
(Burma; Sikhim.)

52. Frontal callus square. Small black species with white haired median abdominal spots. Legs blackish, tibiae yellowish . **leucopogon.**
(India; Sikhim.)

Frontal callus pear-shaped. Large reddish brown species, abdomen with median triangular spots. Legs reddish brown **discrepans.**
(Ceylon.)

Group IX.

53. First posterior cell closed **54**
First posterior cell not closed **55**

54. Large blackish species with narrow fulvous bands on abdomen **servillei.**
(Java.)

55. Abdomen blackish brown, the first two segments covered with grey tomentum (Male) . . . . **crassus.**
(Canara, India; Java.)

56. Forehead narrow, seven or eight times as long as it is broad, frontal callus narrow with a lineal extension. Black or brown species **57**
Forehead broader, four or five times as long as it is broad, frontal callus large with a stout, broad, or spindle-shaped extension **62**

57. Large black or brown species 21 mm. in length, with very narrow pale bands on abdomen **58**
Smaller blackish species, 15 to 17 mm. in length, with whitish bands on abdomen **59**

58. Brown species. Scutellum and sides of thorax with pale tomentum. Legs blackish, tibiae obscurely reddish . . **alboscutatus.**
(India.)

Black species. Scutellum and sides with no such pale tomentum. Legs black, tibiae yellowish white . . . . **explicatus.**
(Sikhim; Assam; India.)

59. Forehead narrower anteriorly. **60**
Forehead hardly narrower anteriorly, but parallel **61**

60. Frontal callus large, reaching the eyes. Antenna, legs, and palpi wholly black. Wings clear or tinged smoky brown . **nicobarensis.**
(Nicobar Islands.)

Frontal callus narrow. Antennae and legs blackish. Palpi yellow. Wings brownish . . . . **justorius.**
(Borneo.)

61. Frontal callus narrow, not reaching eyes. Antennae and legs black. Palpi black, paler on insides. Wings faintly tinged brown . . . . **khasiensis.**
(Assam, Meerut, India.)

62. Brown or black species with whitish bands and spots on abdomen **63**
Reddish yellow species with whitish bands and spots on abdomen **64**

63. Abdomen reddish brown or blackish brown with broad white bands and large triangular median spots. Palpi short and stout . . . . **sanguineus.**
(Bengal; Assam; Malay Peninsula; Java; China.)

Smaller species. Abdomen black with narrow white-haired segmentations and smaller triangular spots. Palpi slender **oxyceratus.**
(Himalayas ; China Hills ; Burma.)

64. Abdomen reddish yellow, darker at apex, with narrower yellowish white segmentations, and median spots. Legs black, tibiae yellowish . . . . **orientis.**
(North India, Nepal, Bhutan.)

Abdomen similar, but the last four segments are black . **fulvimedius.**
(Nepal and Chin Hills; Burma.)

Smaller species. Abdomen similar to that of *orientis*. Legs wholly yellow . . . . **consanguineus.**
(Malabar, India.)

Group X.

65. Black or brown species. Forehead narrower anteriorly, seven to ten times as long as it is broad 66

Large reddish yellow species from 20 to 24 mm. in length. Forehead six to ten times as long as it is broad 72

Dark reddish species from 18 to 22 mm. in length. Forehead seven to ten times as long as it is broad 75

Reddish or reddish yellow species from 16 to 19 mm. in length. Forehead six to ten times as long as it is broad 76

Small species reddish, yellowish, brownish, or blackish, from 12 to 16 mm. in length. Forehead five to ten times as long as it is broad 79

66. Thorax paler than abdomen with yellowish tomentum and pubescence 67

Thorax not paler than abdomen 68

67. Dark brown or blackish species with yellowish brown thorax. Legs black, tibiae white. Wings tinged yellowish brown . **birmanicus.**
(Burma ; Malay.)

Reddish brown species with light yellow or greyish thorax. Legs black, tibiae white, middle and posterior femora yellowish. Wings brownish, clear at apex . . . **flavothorax.**
(Malay.)

68. Wings yellowish brown, yellow on fore border. Black species. Thorax with short red pubescence . . . . . . **tinctothorax.**
(Malay)

Wings brownish or black. Brown or Clack Species 69

69. First posterior cell of wing closed. Abdomen deep black. . **nigrotectus.**
(Siam.)

First posterior cell of Wing not closed 70

70. Blue-black species. Thorax red at base. Antennae reddish brown. Posterior tibia red at base . . . . . . **caerulescens.**
(Java.)

Forehead almost parallel. Abdomen dull reddish brown with greyish blue tomentum. Antennae reddish yellow, black at apex. Tibiae dull red or blackish. Beard and palpi black. **tenebrosus.**
(Canara, India ; Celebes.)

Forehead narrower, not parallel 71

71. Abdomen blackish. Antennae reddish yellow. Tibiae dull reddish. Beard white and black. Palpi yellowish . . . **parakinsis.**
(Malay.)

Abdomen dull blackish, conical. Antennae black. Tibiae black. Beard and palpi black . . . . . . **inobservatus.** (Sumatra.)

72. Forehead parallel, six times as long as it is broad **73**

Forehead narrower anteriorly, eight to ten times as long as it is broad. **74**

73. Broad-bodied reddish-yellow species. Antennae yellow. Legs reddish brown . . . . **fulvissimus.** (Borneo ; Sumatra.)

74. Thorax brownish. Antennae reddish, the third joint black. Femora reddish brown. . . . . **univentris.** (Borneo.)

Thorax yellowish. Antennae, palpi and legs yellow. . . **flavissimus.** (Ceylon.)

75. Abdomen reddish brown, covered posteriorly with yellowish brown tomentum, and yellowish pubescence. Forehead seven times as long as it is broad. Beard white. . . **pauper.** (Sarawak.)

Abdomen dull reddish brown with black pubescence. Forehead seven times as long as it is broad. Beard brownish, scanty. Fore coxae with white hairs . . . . . **leucohirtus.** (Canara, Bombay.)

Abdomen dull reddish brown with black pubescence. Forehead ten times as long as it is broad. Beard brown, thick. Fore coxae with black hairs. . . . . . . **atrohirtus.** (Ceylon.)

76. Forehead ten times as long as it is broad. Frontal callus long and narrow. Abdomen reddish yellow, darker at apex. Legs black, tibiae whitish at base. . . . . . **pallidepectoratus.** (Assam ; Cochin China.)

Forehead six to seven times as long as it is broad **77**

77. Forehead narrowest at the vertex, abdomen reddish. Legs wholly red . . . . **nigropictus.** (India.)

Forehead narrowest anteriorly **78**

78. Abdomen narrow, reddish brown, under side with bands. Thorax reddish. Legs black, tibiae white at base . . **joidus.** (Assam.)

Abdomen conical, reddish yellow, the apex black, underside the same. Thorax blackish. Legs black, fore tibiae dull reddish yellow on basal half, others wholly so . . . **siamensis.** (Siam.)

79. Forehead five times as long as it is broad, narrower anteriorly. Frontal callus club-shaped. Small reddish brown species. Palpi slender, hairy. . . . . **palpalis.** (India.)

Forehead five to six times as long as it is broad, parallel, or nearly so. Frontal callus oblong or club-shaped **80**

Forehead seven to ten times as long as it is broad, narrower anteriorly. Frontal callus long and narrow or oblong **83**

80. Yellow species. Thorax and scutellum covered with grey tomentum and yellow pubescence. Legs and antennae

yellow. Palpi stout, ending in a long fine point. Frontal callus yellowish, often indistinct . . . . **flaviventris.** (Bengal; Assam; Ceylon.)

Reddish brown species. Frontal callus reddish brown, always distinct 81

81. Thorax and scutellum blackish. Palpi slender, long. Antennae black at tip. Legs black, tibiae reddish yellow . . **diversifrons.** (Bengal; Sylhet, Assam.)

Thorax and scutellum usually reddish. Palpi stouter. Antennae not black at tip 82

82. Abdomen reddish brown, unicolourous. Legs reddish yellow, femora often darker. . . . . **subcinerascens.** (Burma.)

Abdomen marked with grey tomentum, giving it the appearance of having zigzag indistinct bands. Legs blackish, tibiae yellowish . . . . **obeonicus.** (Bengal.)

83. Subcallus not bare, shining or tuberculous 84

Subcallus bare, shining tuberculous. 88

84. Palpi stout. Femora black or reddish brown 85

Palpi slender. Femora yellowish 87

85. Forehead two-thirds narrower anteriorly than at vertex. Abdomen yellow anteriorly rather transparent. Legs yellowish, fore legs darker . . . . **borniensis.** (Sarawak.)

Forehead one-third narrower anteriorly than at vertex. Reddish brown or reddish yellow species 86

86. Abdomen reddish brown. Thorax blackish. Legs black, tibiae yellowish wings clear or slightly tinged . . . **fuscicauda.** (Ceylon; Sumatra.)

Thorax reddish yellow, almost same colour as abdomen. Legs yellowish fore femora darker. Wings tinged yellow on fore border . . . . **uniformis.** (Malay.)

87. Abdomen dusky reddish brown or reddish yellow. Forehead about a third narrower anteriorly than at vertex, frontal callus pear-shaped . . . . **subhirtus.** (Bengal; Bombay; Java.)

Abdomen olive coloured. Forehead about half as narrow anteriorly as it is broad at vertex, frontal callus very narrow. **formosiensis.** (Formosa.)

88. Medium-sized species. Abdomen yellowish with darker apex. Palpi yellow. Legs reddish yellow, the fore tarsi darker. Forehead seven times as long as it is broad. . . . **tuberculatus.** (Bengal; Assam.)

89. Small species. Legs black tibiae white. Eyes with cross bands 90

90. Reddish brown or yellowish species. Beard white or yellow. Palpi usually pale. Forehead ten times as long as it is broad . . . . **simplissimus.** (Malay; Sumatra; Java.)

Black, sometimes reddish brown species. Beard black. Palpi blackish. Forehead eight times as long as it is broad. **ceylonicus.**
(Ceylon ; Malay ; Sumatra and Java.)

THERIOPLECTES.

Group XI.

Species with hairy eyes and tubercle on vertex.

91. Forehead with two transverse calli. Subcallus bare and shining. Abdomen black with white haired bands. . . **subcallosus.**
(North India.)

Forehead with one callus. Subcallus not bare or shining **92**

92. Frontal callus black, club-shaped, with spindle-shaped extension. Abdomen black, reddish yellow at sides of first two or three segments. Palpi stout with short apex. Appendix usually present. Legs black and reddish yellow . . . **hirtus.**
(North India.)

Frontal callus small, indistinct. Abdomen blackish, only reddish on second segment. Palpi slender with long acute apex. No appendix to wing **93**

93. Smaller species. Legs black and reddish yellow . . . **wyvillei.**
(Naranda, Himalayas, where it bites human beings.)

Frontal callus broad, yellow. Abdomen black, reddish yellow at sides. Palpi slender. No appendix to wing. Legs yellow . . . . **albilateralis.**
(Java.)

Tabanus striatus, Fabr. A medium-sized fly; antennae yellowish red, darker at their apices; palpi pale yellow. Frontal callus oblong, not quite touching the eyes in front and receding from them behind; for a short distance it is not more than a fine line, afterwards broadening out; the vertical extension often starts from the callus as a broad stripe. Thorax brown with four distinct greyish lines. Abdomen long and slender, reddish to blackish brown in colour. The medium light stripe extends to the sixth segment, and is formed of oblong spots, narrowest at their apices. The lateral light stripes extend to the fourth segment, and there is often an additional spot on the fifth segment. Male with a broad bluish grey band, intersected by a narrower band, running across the eyes; abdomen markedly pointed, with lateral pale stripes extending to the third segment only. A common species, widely distributed in India.

Tabanus albimedius, Walker. A large species with a broad abdomen. Antennae reddish, with dark apices; palpi pale yellow. Frontal callus not quite reaching the eyes, with a narrow linear extension. Thorax reddish with indistinct grey lines. Abdomen reddish brown with a light median stripe extending the whole length; the area on the first segment

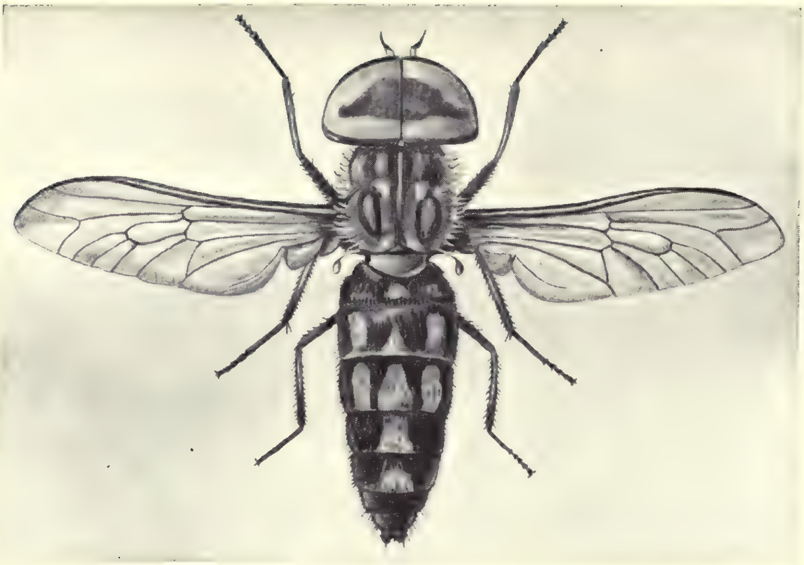


Fig. 1.

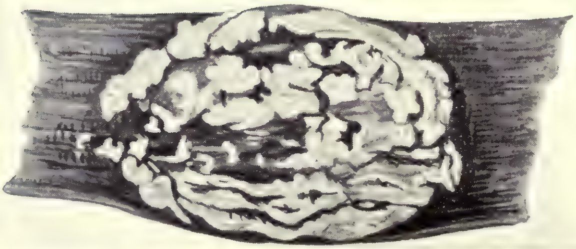


Fig. 2.

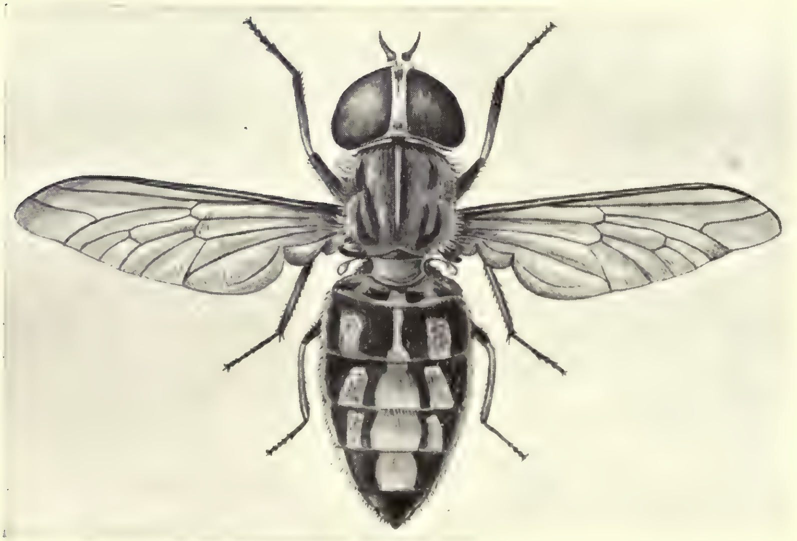


Fig. 3.

PLATE XL

Figure 1. *Tabanus speciosus*, ♂. ×3.

Figure 2. Egg mass of same; note the chalky substance obscuring the eggs.

Figure 3. *Tabanus speciosus*, ♀. ×3.

small, that on the second flask-shaped, the remaining areas of the stripe triangular; the lateral stripes extend the whole length, but are broadest on the second segment. The male is difficult to distinguish from that of *striatus*: it is darker, and the brown intersecting band across the eyes is much wider; the median abdominal light stripe is much broader in parts and is not so uniform. This is one of the commonest Indian species, and occurs almost all the year round in Madras.

Tabanus speciosus, Ricardo (Plate XL). A large handsome fly, which may at first sight be confused with *albimedius*. Antennae reddish, with dusky tips; palpi yellow with many black hairs. Frontal callus oblong, not reaching to the eyes, its backward extension narrow, sometimes indistinct. Thorax greyish red or brown, with five distinct grey stripes, the median one very narrow. Abdomen brownish black with a median light stripe consisting of five spots, of which the first is small, the second flask-shaped, the third triangular, the fourth triangular but broader, the fifth nearly oblong. There are four lateral pale spots, of which the first is indistinct, the others well marked and obliquely elongated. Male very similarly marked, except that the median stripe is less distinct and that there is no lateral spot on the fourth segment. Eyes with a broad intersecting band, which becomes narrower at the sides. This is a rather rare fly in Madras. It feeds on cattle side by side with the other two species.

GENUS CHRYSOPS, MEIGEN.

Small Tabanidae *with long antennae and banded and beflecked wings. The males are somewhat differently marked to the females. In the female the eyes are bare, and are widely separated; there are three well marked ocelli on the vertex, and shining black tubercles on the face. The second joint of the antenna is usually as long as the first; the third is four-jointed and simple. The palpi in the female are long and bullet-shaped; in the male they are short and stumpy. Thorax as broad as the head. Abdomen ovoid, with yellow bands and dark stripes. The wings are dark and are ornamented with brown cross bands.*

The conspicuous markings of the flies of this genus, their long antennae and well marked ocelli, render them easy to recognize. The eyes in the females of many species exhibit in life the most brilliant patterns of green, purple and gold, and are most beautiful objects; the same markings are often present in the lower smaller-facetted area of the eyes of the male. In some species the eyes are very large and are markedly holoptic; in others they are distinctly small and more or less dichoptic.

The species are abundant in the Ethiopian and Oriental regions, and in North and South America. As a group they are retiring in their habits; they are found chiefly in well-wooded localities and in low lying shrub in the vicinity of water. The females are blood-suckers, and feed upon cattle and horses.

Miss Ricardo gives the following Key to the Oriental species:—

KEY TO THE ORIENTAL SPECIES OF CHRYSOPS

1.	Wings with a dark transverse band and an apical spot	2
	Wings with a dark transverse band but with no apical spot	11
2.	Wings with a hyaline sinus on the posterior part of the band, in the fifth posterior cell	3
	Wings with no hyaline sinus on the posterior part of the band, in the fifth posterior cell	7
3.	Abdomen blackish, yellow at apex, with grey bands on the first two segments and a grey median stripe	**manilensis.** (Manila.)
	Abdomen yellowish with black stripes	4
	Abdomen black, whitish, or yellowish at base	6
4.	Discal cell hyaline. Abdomen with four long black stripes	**mlokosiewiczi.** (China; Japan.)
	Discal cell not hyaline	5
5.	Abdomen with a short black bifid stripe on the second segment, often extending to the third or fourth segment	**dispar.** (Widely distributed in India; Ceylon; Malay and adjacent parts.)
	Abdomen with a bifid stripe on the second segment and a network of black markings on the third segment, leaving only three yellow spots free	**designata.** (North India; Western China.)
6.	Abdomen whitish on the first four segments, apex black	**rufitarsus.** (Java.)
	Abdomen black, the first two segments largely yellow, the second and third segments with small median spots. Face yellowish. Apical border of band of wing straight, concave.	**translucens.** (Malay; Java.)
	Abdomen black, the second segment yellowish on fore border. Face blackish. Apical border of band of wing straight	**pellucida.** (South India.)
	Small species, abdomen blackish, the first two segments yellow anteriorly. Face black	**alter.** (Borneo.)
	Large robust species. Abdomen blackish with paler median spots, largely yellow on the basal segments. Face yellowish. Apical border of wing irregular	**sinensis.** (China.)

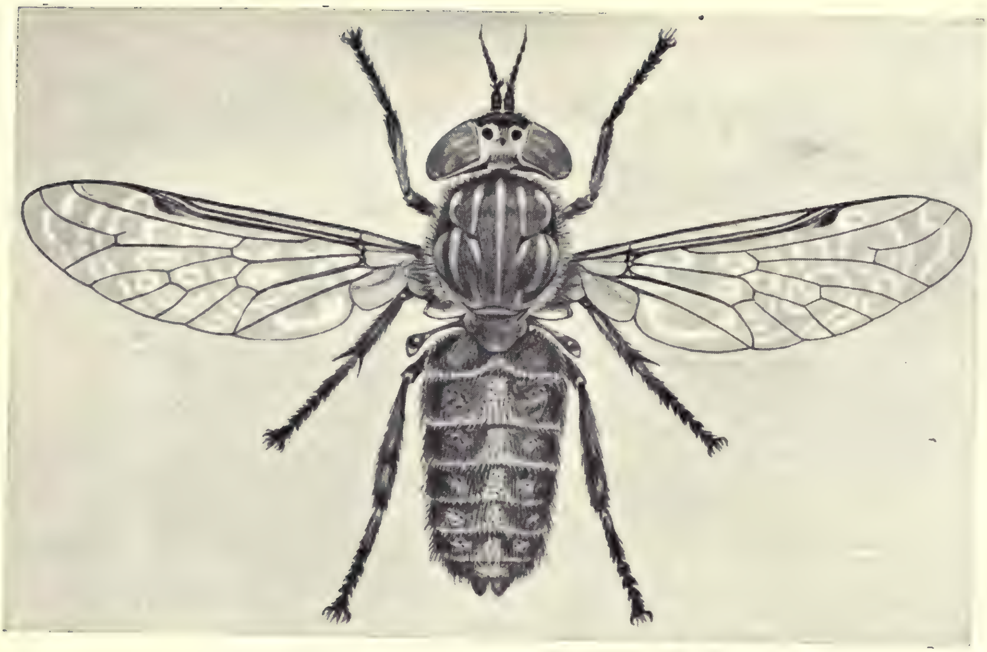


Fig. 1. Haematopota pluvialis, ♀. × 6.

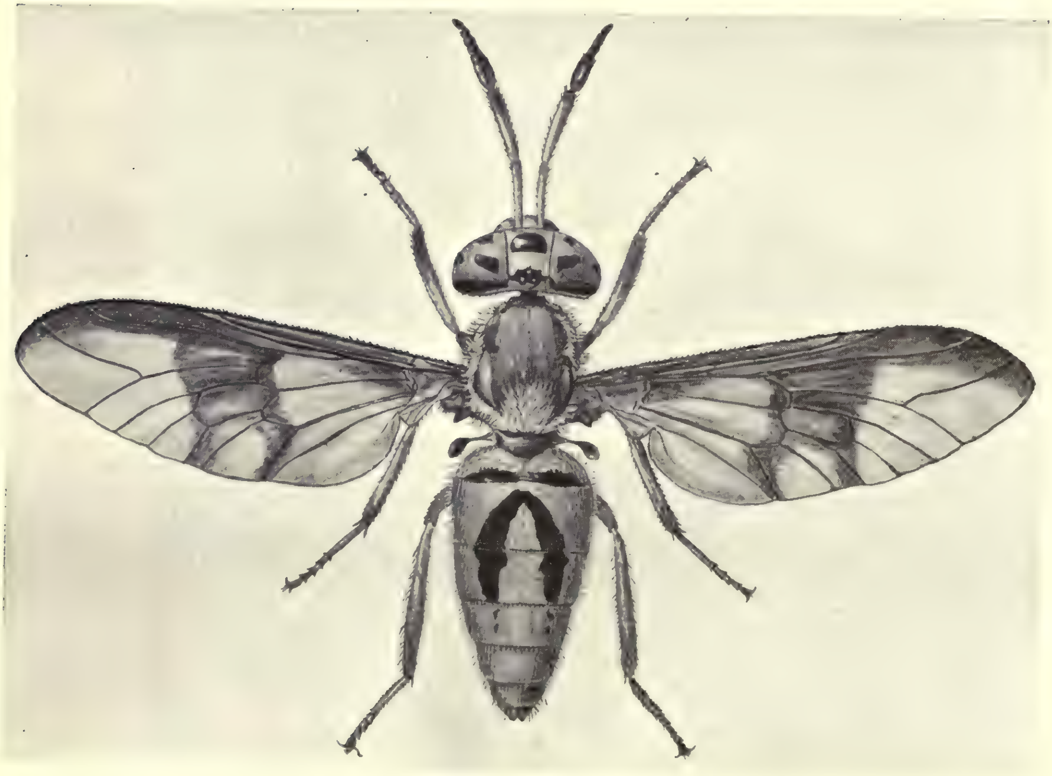


Fig. 2. Chrysops dispar, ♀. × 7.

7. Wings with a clear spot in the discal cell, first joint of the antenna slightly incrassate. Abdomen blackish with pale spots . . . . **stimulans.**
(Bengal.)
Wings with no clear spot in the discal cell 8
8. Band of wing broad throughout. Abdomen yellow with a black bifid stripe in the second segment . . . . . **indiana.**
(South India ; Assam.)
Abdomen yellowish, with a black band in the middle 9
Abdomen yellowish, with two distinct black bands 10
9. Abdomen with blackish legs and face . . . . . . **fasciata.**
(Malay ; Java ; Sumatra.)
Abdomen with yellowish brown legs and face . . . . **fixissima.**
(Ceylon ; Sarawak.)
10. Abdomen with the black bands narrower . . . . . **signifer.**
(Philippines.)
Abdomen darker, the black bands broader . . . . . **cincta.**
(Malacca ; Philippines.)
11. Abdomen black with a yellowish band on the second segment. Small species . . . . **flavocincta.**
(Assam ; Ceylon ; Sarawak.)

Chrysops dispar, Fabr., (Plate XLI, fig. 2) is a common South Indian species, easily distinguished from the others by the colouration of the abdomen, which is yellow, with a dark bifid stripe commencing on the second segment and extending to the fourth. *Chrysops dimidiata*, van der Wulp, a West African species, is said to enter houses and to bite man.

It has been announced recently that Leiper has demonstrated that the development of *Filaria loa* is completed in the salivary glands of a species of *Chrysops* in Calabar, Southern Nigeria.

GENUS HAEMATOPOTA, MEIGEN

Medium sized or small flies with elongated bodies and with light and dark markings on the wings. Head transversely oval, and distinctly broader than the thorax ; the eyes may be hairy or nude ; in the female they are widely separated. The antennae are three-jointed ; the first joint is thick and moderately long, the second very short, the third longer than the first two together, and consisting of three segments incompletely separated from one another. The thorax is rounded and may be marked with bands or spots. The abdomen is elongated with parallel sides. The wings are long and of a dark brown or black colour, and may have three or more rosettes formed by pale marks on a darker ground colour.

In most of the females of this genus the eyes are highly coloured, and, as the markings have been employed to a considerable extent in separating the species from one another, they should be noted in the fresh condition and recorded. As a rule the eyes of the males have no bands on the dorsal portion, but are marked like those of the female in the lower area where the facets are smaller.

The flies of this genus are widely distributed, and many of the species are common where they occur. *Haematopota pluvialis*, L., which is figured on Plate XLI, is perhaps the commonest European species. A large number are found in the tropics, Africa being notably rich in species. According to Neave the African species are more abundant in higher localities; they have been found at an altitude of 10,000 feet. Neave points out in a recent paper that the East African species are somewhat irregularly distributed, being abundant in some parts and rare in others, and that the season in which they are prevalent is very short. He shows that the lighter species are found mainly in open short grass country, while the darker ones are confined to well-wooded localities in the vicinity of streams.

GENUS SILVIUS, MEIGEN

Medium-sized flies with clear hyaline wings. Antennae short, the second joint much shorter than the first; the third segment has a well developed dorsal tooth at its basal end, and consists of four segments. The eyes are uniformly coloured and the facets are all of one size in both sexes.

The species of this genus are widely distributed. The females are blood-suckers, but are not aggressive unless their haunts are approached. Neave states that the female of *S. fallax*, Austen, frequents water holes and attacks the natives as they go to draw water.

GENUS CADICERA, MACQUART

Large robust flies with dark wings. The head is flattened antero-posteriorly. The abdomen is broadened laterally, and is generally brightly coloured. Antennae three-jointed, simple, and without a spur; the distal joint has seven annulations. The proboscis is as a rule longer than the head.

Most of the species of this genus are confined to South Africa, but some have been recorded from other parts of the same continent. One species is known from Nyasaland, and another, *C. speciosus*, Austen, has been found by Neave in German East Africa; the latter was taken in wooded country at the foot of Mount Kifulufulu, and was seen to bite cattle.

GENUS PANGONIA, RONDANI

The flies of this genus are distinguished by the remarkable long forwardly-directed proboscis. The great majority of the species, perhaps all, are flower feeders. The genus has been divided into five subgenera, according as to whether the first posterior cell is open or closed, the eyes bare or hairy.

PANGONIA (sensu restr.) Most of the species included in this subgenus are large insects with hairy bodies. The antennae are simple, the first joint short, the third long, with seven annulations. The proboscis is long and slender, and may be as long as the body of the fly; that of *P. rostrata*, for instance, is one and a half inches long. There is evidence that some of these flies, notwithstanding the great length of the proboscis, feed on mammalian blood; they do so, not by settling on the skin in the ordinary manner and inserting their biting parts deliberately, but while hovering near by, making sudden darts; to obtain a full meal it must be necessary for them to repeat the manœuvre many times. Such a habit is apparently exceptional in the genus, as in the majority of cases the mandibles and maxillae are shorter than the labium, and cannot, therefore, be employed in making a wound. The species are mainly found in the Ethiopian region.

EREPHROSIS, Rondani. In this subgenus the first posterior cell is closed and the eyes are hairy. The species are found in South America and parts of Australia. Lutz and Neiva have recently described a beautiful golden species from Brazil. It is not known whether they are bloodsuckers or not.

SUB-PANGONIA, Sourcouf. This subgenus closely resembles *Pangonia*, except as regards the proboscis. This is short or moderately long, and is thick and fleshy; it is bent downwards at an obtuse angle. The labella are as long as the proboscis, and are conspicuously thickened. On the superior margin of the inner surface of each labellum there are ten rod-like structures, thick at the base and pointed apically, which Sourcouf thinks are almost completely closed tubes which assist in suction. Austen states that *Dorcaloemus silverlocki*, Aust., and *Pangonia comata*, Aust., have homologous structures on their labella. Only two species of *Subpangonia* are known, *S. gravoti*, Sourcouf, and *S. grahami*, Aust., the former from the French Congo and the latter from Southern Nigeria. They may be mistaken for humble bees, as they have the habit of hovering in the air, and their flight is accompanied by a bee-like buzz.

DIATOMINEURA, Rondani, and CORIZONEURA, Rondani, are found in the Ethiopian region, the latter also in the Oriental region. They are not aggressive blood-suckers, and are found in well-wooded districts.

Genus DORCALOEMUS, Austen. The flies of this genus have bare eyes and have the posterior cell closed. They are not aggressive biters. The genus is limited to South Africa.

Genus RHINOMYZA, Wied. This genus has a superficial resemblance to *Chrysops*. The antennae, however, resemble those of *Tabanus*, the basal hook being well marked. Ocelli are present, and the hind tibiae have spurs. They are found in Africa, Java and South America. Neave states that they frequent shady places and feed most frequently in the evening.

Other genera of Tabanidae

The remaining genera of the Tabanidae are distributed as follows :—*Udenocera*, Ricardo, Ceylon.—*Neotabanus*, Ricardo, Ceylon.—*Diachlorus*, Osten Sacken, North and South America and the Philippines.—*Lepidoselaga*, Macquart, Brazil, Australia and Chili.—*Stibasoma*, Schiner, Brazil.—*Dasybasis*, Macquart, Australia and Chili.—*Bolbodimyia*, Bigot, Venezuela.—*Acanthocera*, Macquart, South America.—*Dichelacera*, Macquart, South America.—*Apocampta*, Schiner, Australia.—*Dicrania*, Macquart, Brazil. *Pityocera*, Gigl-Tos, Central America.—*Goniops*, Aldrich, North America. —*Apatolestes*, Williston, North America.—*Pelecorhynchus*, Macquart, South America and Australia. *Pronopes*, Loew, Cape of Good Hope and Java.—*Esenbeckia*, Rondani, Brazil.—*Gastrixodes*, Saunders, India.—*Adersia*, Austen, South Africa,—*Aegophagamyia*, Austen, Zanzibar, Rodrigues, and Astove Islands ; British East Africa.—*Bovierella*, Surcouf, Madagascar.—*Scepsis*, Walker, South America.—*Selasoma*, Macquart, South America.—*Scione*, Walker, Seychelles, South America and Australia.

Bionomics of the Tabanidae

When studying the feeding habits of the blood-sucking Tabanidae it is useful to have a tame cow or horse, and to tether it in a field or some well-wooded place in the vicinity of water in a locality in which the flies are known to occur. In a short time one or more of the females will alight on it and commence sucking blood. The different species which have been observed under such conditions in Madras show a remarkable peculiarity in the selection of the site from which to feed. *T. specious* and *T. albimedius* almost invariably settle low down on the back of the hind leg, while *T. striatus* and *T. hilaris* frequently select the same site, but may also be seen biting on the under surface of the abdomen, particularly on the flap of skin near the navel. *T. bicallosus* seldom settles on the lower parts of the body but nearly always on the sides of the neck or abdomen. *T. ditaeniatus* is most often seen biting on the udder, sometimes however, it will settle on the side of the neck. *Chrysops dispar* generally chooses the inner sides of the fore legs, and *Haematopota* the hump or the neck.

If one of these flies is watched closely as it feeds, it will be noted that as it becomes replete with blood it passes out a dark fluid—if it has fed recently—which drops on to the hair of the host. Next a clear fluid is voided, and last of all apparently unaltered blood. All this fluid collects in droplets on the hair below the fly. The moment it withdraws its proboscis one or two large drops of blood trickle out of the wound and mix with the excreta. It is not unusual to see two or even three flies feeding at the same time close together. These habits probably explain how tabanids become infected with their natural flagellates (*Crithidia* and *Herpetomonas*). A fly which sucks blood at the spot where the excreta of another has been deposited must necessarily contaminate its labella when they are pressed against the skin just before the wound is made. Immense numbers of flagellates are passed out in the fluid excreta of an infected fly, and it is not difficult to understand how another fly may suck them up. For the description of the method of feeding, see page 27.

On leaving the host the flies usually settle on the under surfaces of leaves, the barks of trees, stones, or the walls of an adjacent building; they remain here for several hours, and later collect in the vicinity of water. Judging from experiments carried out with tabanids kept in captivity, they appear to feed every three days. It is not definitely known whether copulation takes place before the first feed of blood, but it would appear that fertilization is in some way connected with the subsequent food of the female. No satisfactory explanation can be offered as to why bred females can hardly ever be induced to suck blood, even when they are placed in a large enclosure along with cattle. It is interesting to note Neave's observations on the habits of these flies when the males predominate. He says, 'I think it very probable that female Tabanidae 'will be found to feed on blood only during a certain period of their imago 'stage. This period seems to be subsequent to pairing and to the death 'of the male individuals, and most probably (though I have no actual 'evidence of this) before oviposition'. Although numbers of both sexes of *T. albimedius* and *T. striatus* have been kept in large cages by the writers, under as near as possible natural conditions, the act of copulation has never been seen, and the majority of the females would not suck blood. It is not known how long a tabanid lives under natural conditions. Observations on this point would be most valuable.

Hine records having seen *T. sulcifrons* in copulô about 8 a.m.; the male clings to its perch, and the female hangs suspended with its legs and wings motionless; the whole act lasts about ten minutes. When disturbed the male flies a short distance, and soon alights either on the ground or on some low-lying foliage.

It has frequently been noted that tabanids are in the habit of flying over water, and darting down and striking the surface; these manœuvres are not very clearly understood, but Hine appears to think that both sexes behave in this way and that they are merely sipping water. Hine also considers that the female tabanid takes much food other than blood, and that some may even pass their whole existence without taking blood at all; he has examined the alimentary tracts of both sexes and found a yellow fluid, indicating that something else besides pure water or blood had been imbibed.

Breeding Habits and Early Stages

The Tabanidae always lay their eggs in the vicinity of water, and the flies are never found very far from it. The habits of those species which have been studied show that there is considerable variation in the methods of egg-laying. Some species oviposit almost entirely on particular plants, while many do not select any special plant. The position in which the eggs are deposited with respect to the depth of the water depends to a large extent on the structure of larvae; this is a point which would repay further study.

Hine has described the egg-laying habits of *Tabanus stygius*, Say, which always oviposits on the upper surfaces of the leaves of the arrow plant, placing the eggs above the point where the petiole meets the expanded part of the leaf. Hine goes on to say: 'So closely is this habit followed that a hundred masses of eggs are found thus located, to one placed otherwise. Sometimes a mass is observed on a leaf of another plant, but in the same location, and once in a long time eggs are seen in a different location of a leaf'. The black horse fly, *Tabanus atratus*, Fabr., places its eggs on a particular species of sedge in low ground near swamps or ponds. *Chrysops callidus*, Osten Sacken, arranges its eggs in a single layer on leaves of various kinds of plants overhanging water in ponds and small lakes; *C. moerens*, Walk., oviposits is similar places.

King has recently recorded the egg-laying habits of several Soudanese tabanids; *Tabanus par*, Walk., and *T. taeniola*, Pallisot de Beauvois, for instance, lay their eggs on the leaves of water weeds, and on blades of grass. *Tabanus kingi*, Aust., lays its eggs on rocks over deep pools.

In Madras, *Tabanus albimedius*, Walk., oviposits in a variety of situations, but most frequently on the leaves of some plant overhanging deep water. Its egg masses have also been found on small rocks in the bed of a stream, and on pieces of string hanging over house drains; on one occasion a mass was found on a Papaya tree, at the foot of which water was occasionally allowed to flow. *Tabanus speciosus*, Ricardo, always lays its eggs on the leaves of water lilies growing in deep water. *Tabanus striatus*, Fabr., oviposits as a general rule on blades of grass, pieces of stick, etc., at the edge of a river, stream or pond; *Tabanus hilaris*, Walk., has the same habits. *Chrysops dispar*, Fabr., *Tabanus ditaeniatus*, Macq., *Tabanus bicallosus*, Ricardo, *Tabanus virgo*, Wied., and two undetermined species of *Haematopota*, all of which are small tabanids, invariably lay their eggs on blades of grass just at the edge of a shallow stream, or on the leaves of the lotus plant at the edges of small ponds, but never over deep water.

The position selected by any one of these flies to deposit their eggs is not a chance one. The larvae of the larger tabanids, such as *albimedius*, *striatus*, and *speciosus*, are powerful swimmers and have air sacs connected with their tracheal tubes, so that they can float or sink at will. The larvae of the smaller species in Madras are devoid of these air sacs, so that if they fall into deep water they die. It is important to recognize this in breeding experiments and to place them in trays with only a little water.

The number of eggs laid by the different species is also of interest. *T. albimedius* and *T. speciosus* lay between 500 and 600 eggs, while the smaller species lay about 300. When one of the larger species is about to oviposit it alights on the leaf or blade of grass with its head downwards; it then thrusts the tip of its abdomen forwards under its thorax, and deposits an egg, which adheres to the leaf owing to the sticky substance which accompanies it. The abdomen is then returned to its original position, and as soon as the next egg is ready to be laid, is again flexed, and the second egg is placed at one or other side of the first. In this way three or four eggs are laid on one side of the first and three or four on the other. The mass at this stage has the shape of a V. The fly now moves forwards, and, raising the end of her abdomen to one arm of the V, places a number of eggs down the side until the apex is reached; she then changes over to the other side and deposits eggs all down that arm up to the apex. In the end a raised compact mass of eggs is built up, which, if examined with a lens, demonstrates the precision with which the eggs are placed in reference to one another.

It is often possible to watch a female tabanid with a hand lens while she is laying her eggs without disturbing her; sometimes it is even possible to break off the leaf or twig and to carry her some distance to a laboratory, where she will continue to lay her eggs.

In Madras all the smaller species of *Tabanus*, as well as *Chrysops dispar* and the two species of *Haematopota* referred to above, spread their eggs out in one or more layers on blades of grass; in some instances they are moulded into the hollow of the blade right up to the tip (Plate XLII, figs. 2, 11 and 12). *Tabanus speciosus* (Plate XL, fig. 2), instead of forming a V-shaped mass as is usually the case with the larger tabanids, lays its eggs in a round heap, which it then plasters over with a chalk-like substance, almost completely covering the eggs.

The eggs of all the smaller tabanids in Madras are torpedo-shaped, while those of the larger species, such as *albimedius*, are sub-cylindrical with tapering ends. The eggs of *Tabanus bicallosus*, a small species, measures 1·1 mm. in length and ·2 mm. in breadth, that of *ditaeniatus* is about 1·2 mm. in length and also ·2 mm. in breadth; the eggs of *albimedius*, a larger fly, measure 1·9 to 2 mm. in length and ·4 mm. in breadth. Most of the eggs of the smaller species are white when first laid, but they soon become dark. Those of one species of *Haematopota* are dark grey when deposited, while those of *albimedius*, *striatus* and *hilaris* are brownish white.

The egg masses of tabanids are often parasitized by small species of hymenoptera which oviposit in them. *Phanarus tabanivorus*, Ashmead, is common in the United States, where, according to Hart, it parasitizes a large number of the egg masses of *Tabanus atratus*. *Telenomus benefactor*, Crawford, is another chalcid which parasitizes the eggs of tabanids in the Soudan. In Madras a similar insect, which has not been identified, regularly destroys large numbers of egg masses of *albimedius* and *striatus*. A parasitized egg mass can be recognized by the almost black colour which it assumes when the development of the embryos of the hymenopteron is almost complete.

In Madras the smaller species of Tabanidae always lay their eggs in the afternoon, commencing about 4 p.m.; *Chrysops dispar* has been seen ovipositing as late as 7 p.m. The larger species, on the other hand, lay their eggs any time during the day, but as a rule in the morning. The larvae hatch out in from four to seven days after the eggs are laid;

PLATE XIII

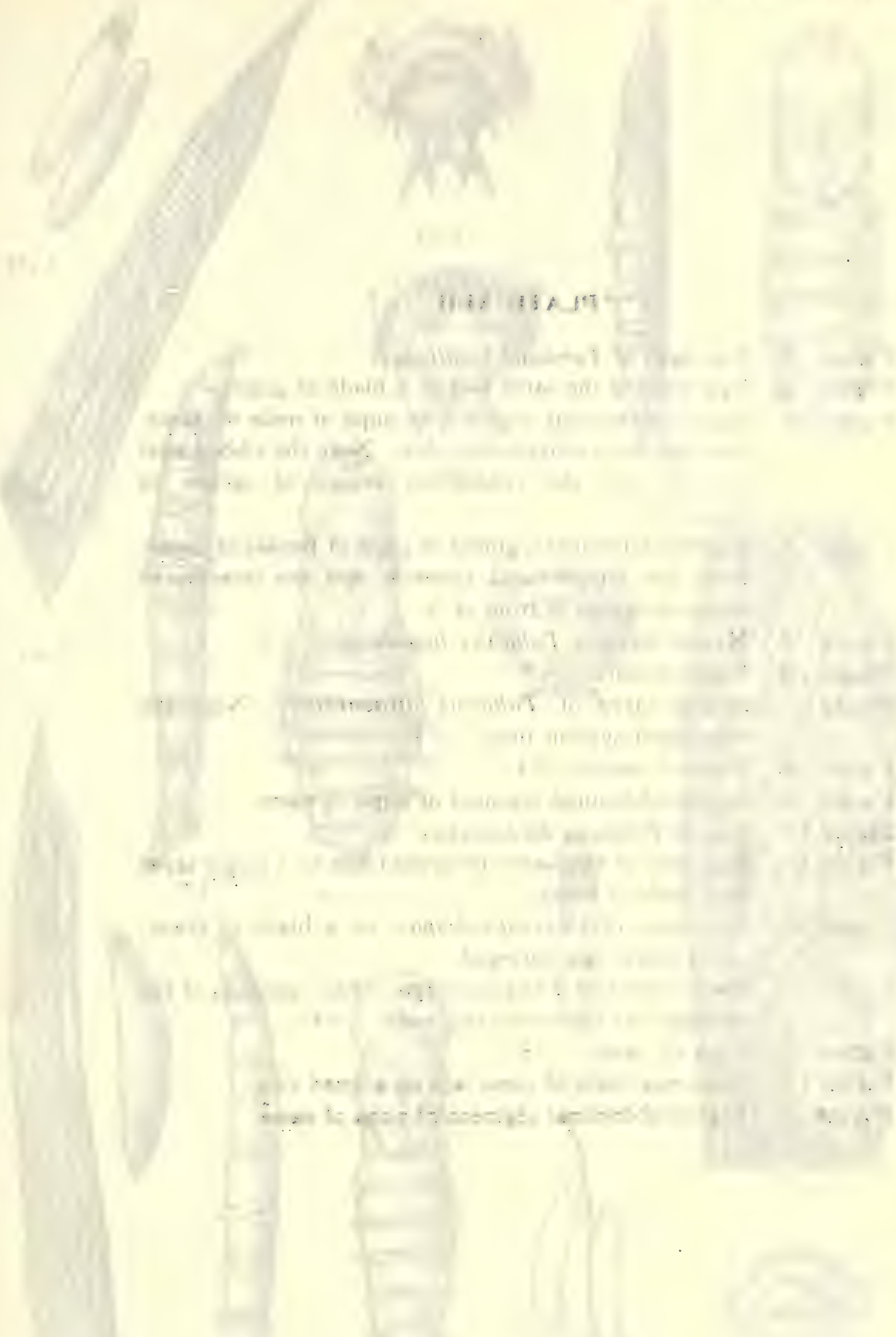


PLATE XLII

Figure 1. Two eggs of *Tabanus bicallosus.*

Figure 2. Egg mass of the same laid on a blade of grass.

Figure 3. Eighth abdominal segment of pupa of male of same, showing the six large tubercles. Note the ribbed anal tubercle and the continuous fringe of spines in front of it.

Figure 4. Eighth abdominal segment of pupa of female of same. Note the simple anal tubercle and the interrupted fringe of spines in front of it.

Figure 5. Mature larva of *Tabanus bicallosus.* × 3.

Figure 6. Pupa of same. × 4.

Figure 7. Mature larva of *Tabanus ditaeniatus.* Note the short stout syphon tube. × 3.

Figure 8. Pupa of same. × 4.

Figure 9. Eighth abdominal segment of pupa of same.

Figure 10. Egg of *Tabanus ditaeniatus.*

Figure 11. Egg mass of the same fly spread out in a single layer on a blade of grass.

Figure 12. Egg mass of *Chrysops dispar,* on a blade of grass; also a single egg enlarged.

Figure 13. Mature larva of *Tabanus virgo.* The openings of the tracheae are flush with the body. × 4.

Figure 14. Pupa of same. × 5.

Figure 15. Small egg mass of same laid on a dried twig.

Figure 16. Eighth abdominal segment of pupa of same.

PLATE. XLII.

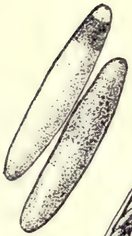


Fig. 1.

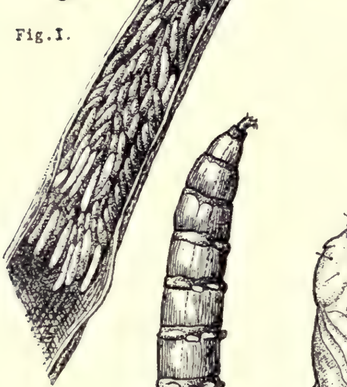


Fig. 2.

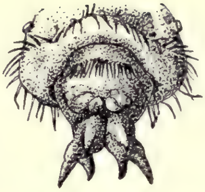


Fig. 3.

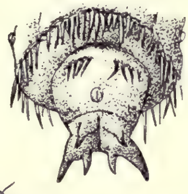


Fig. 4.

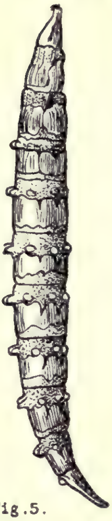
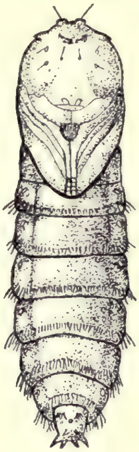


Fig. 5.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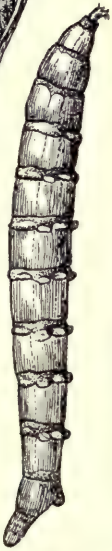


Fig. 7.

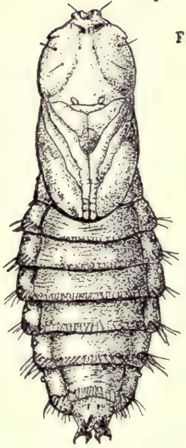


Fig. 8.

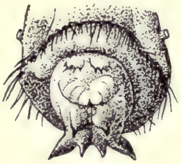


Fig. 9.

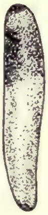


Fig. 10.

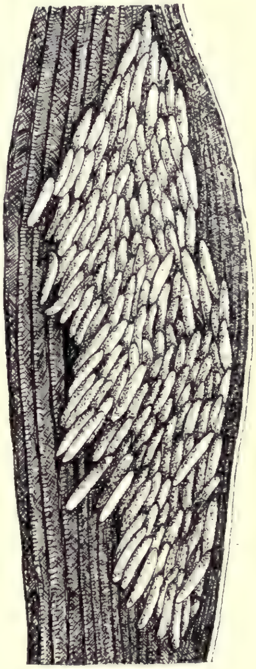


Fig. 11.

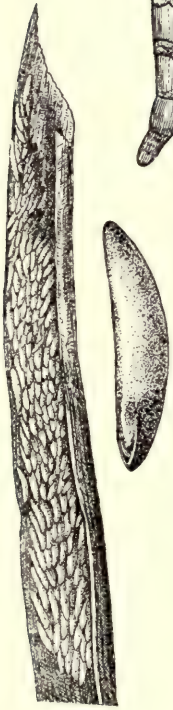


Fig. 12.

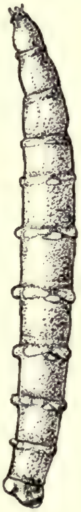


Fig. 13.

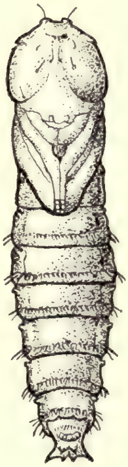


Fig. 14.

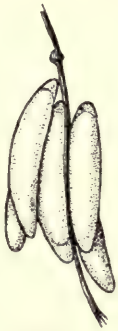


Fig. 15.

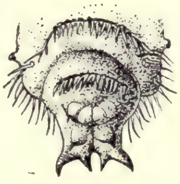


Fig. 16.

first one larva wriggles out and very soon afterwards the others emerge and the mass is transformed into a collection of larvae struggling to free themselves; they drop singly or in heaps into the water or wet mud, and quickly bury themselves out of sight. The recently hatched larva is almost pure white, and both ends are, as a rule, pointed.

External structure of mature larva, Plate XLII

The body of the mature larva is cylindrical, tapering at both ends, and consists of eleven segments excluding the head; its skin may be blotched or streaked in the form of stripes or bands. The antennae are three-jointed, the basal joint being short, and are attached to the anterior angles of the head just above the palpi; a bunch of stiff spines, either short or moderately long, is situated just above each antenna and on each side of the labrum. The segments of the body are whitish or striated, and the prothorax has a groove on its ventral surface. Each segment of the abdomen has a Y-shaped group of punctures and is encircled anteriorly by a horizontal ridge beset with fine hairs. There are two prominent fleshy tubercles at each lateral angle, and four, arranged in pairs, on the ventral surface. The last segment has a bilobed anal prominence bounded posteriorly by a semicircular ridge covered with hairs. The vertical stigmal plate is situated at the apex of a conical retractile prolongation, the syphon tube.

The mouth parts

The mouth parts of the larva are adapted for seizing the prey, and constitute a very formidable apparatus. The essential organs are the mandibles and first maxillae, and of these the former are the most powerful weapons. Each *mandible* is a stout rod of chitin, slightly expanded at the base, to which the muscles are attached, and narrowed distally to a blunt point; the rod is curved downwards and forwards, and is armed on its concave border with many coarse serrations. The *maxillae* are similar in shape and general disposition, but are smaller and less heavily pigmented, and are more pointed. Both pairs of appendages can be thrust out of the head in a downward and forward direction when the larva attacks its prey, by means of the protractor and retractor muscles attached to the bases of the rods. One sometimes becomes unpleasantly aware of the existence of these organs when handling the larvae, as they are used in defence as well as in attack, and are capable of inflicting a sharp nip, though they do not draw blood. The *maxillary palps* are simple and two-jointed, the distal joint being much smaller than the proximal one. The dorsal and distal extremity of the head is produced forwards as a short and fleshy labrum.

The Alimentary Canal, Plate L, fig. 1

The *pharynx* is an elongate chitinous chamber of the usual type, and is easily seen in the living larva. It leads posteriorly to the *oesophagus*, which is wider and more muscular than that of the adult: it is usual to find that the oesophagus is wider and more muscular in insects whose food is solid or semi-solid than in those which take only fluid food. The oesophagus opens into a short and cylindrical *proventriculus*, which is also a highly muscular structure, and is sharply distinguished from the succeeding part of the gut by its clear translucent appearance in the fresh condition. The *mid-gut* extends from the proventriculus to the hind end of the body, and is thrown into one or two simple coils, not constant in their position. It is separated from the proventriculus by a short constriction, and is again constricted at the posterior end, just anterior to the opening of the Malpighian tubes. Between these points the lumen is wide, and is thrown into numerous sacculations by the contractions of the muscle fibres in the wall. The mid-gut is of a very striking orange red colour in the fresh condition, and is filled with a semi-solid mass of a light chocolate colour, which oozes out if the wall is punctured in dissection. The *hind-gut* is short and simple, and is coiled up in the posterior end of the abdomen. The total length of the gut is about twice the length of the body of the larva.

To dissect out the alimentary tract :—Pin the larva down in a dissecting trough, extending it as much as possible. Then take a pair of fine forceps and pinch up a portion of the integument near the anterior end, and cut it with a pair of fine scissors. Once the initial incision has been made it is easy to cut a strip of the integument away from the rest, carrying the incision to the opposite end of the body. The large lateral tracheae should now be torn off at the posterior end and removed. The whole of the alimentary tract is then exposed, and is easily separated from the integument, to which it is only attached by a few tracheal twigs.

The *salivary glands* are simple and tubular, and bear a remarkable resemblance to those of the adult insect.

The Respiratory System

The *respiratory system* resembles that of the mosquito larva. There are two large lateral tracheae which run the whole length of the body, on each side of and slightly dorsal to the alimentary canal. These communicate with the external air through an opening, which can be closed, on a small eminence on the dorsal surface of the penultimate segment. As they pass forward they give off branches for the supply of the tissues in the ordinary manner; they are not, however, simple tracheae, but are rather of the nature of air sacs, as their diameter in most species is distinctly greater than would suffice for their main function of conveying air to the tissues, and contracts suddenly, without the giving off of any branches, at the anterior end. In some species such dilatations are not present.

Graber's organ

At the posterior end of the larva of *Tabanus* there is a curious structure, the function of which has not been determined. It consists of a small pear-shaped sac, the broadest end of which is anterior; the posterior end narrows down to a fine tubule, which opens on the integument of the body between the last and the penultimate segment. Within this sac there is a series of capsules set one behind the other in the long axis, and within each of these capsules a pair of small black pyriform bodies, each attached to the anterior side of the capsule by a delicate pedicle. These bodies diminish in size from the anterior end, the first being considerably larger than the rest. They are easily seen through the integument in the living larva. Graber believed that the structure is a sense organ, but Berlese does not consider that this has been proved to be the case. It is well supplied with nerves. The outer sac is an invagination of the integument, and as such has a chitinous lining.

The pupa. Plate XLII, figs. 6, 8 and 14

The *pupa* is sub-cylindrical, abruptly pointed anteriorly, and tapering somewhat posteriorly; it is generally yellowish brown to ferruginous brown, finely wrinkled, and has a lateral tuft of hairs on each abdominal segment. On either side of the head are the antennal sheaths, pointing outwards, and on each side of the median line two large tubercles, each with a central hair; below these there are two raised areas with sharp edges, separated by a deep ridge. Lower still there is a pair of elevations, also with raised edges, and on the ventral surface of the head one or more tubercles. The segments of the thorax are indistinct; the mesothorax bears the large, raised ear-shaped spiracles. The abdominal segments are free and about equal in length, and have one or more hairs near their hind margins; the second to the seventh segments inclusive have well-marked lateral ridges, covered with long hairs which are continued into the dorsal and ventral surfaces. These hairs increase in length from before backwards, and are best developed on the seventh segment. The eighth segment is short, and is armed with six projecting spurs or teeth, and with a large anal tubercle. In the male the tubercle is ribbed and bounded anteriorly by a continuous fringe of strong spines; in the female the tubercle is smaller and the fringe of spines is broadly interrupted (Plate XLII, figs. 3, 4, 9 and 16). The pupae of many of the larger species of *Tabanus* have in addition a lateral tuft of spines situated on a ridge.

Tabanid larvae grow very slowly, feeding at first on small crustaceans, which are abundant in water and moist earth; they soon, however, attack and destroy each other, and this is one of the greatest obstacles in breeding experiments. In Madras, the larvae take from two and a half to three and a half months to become mature, and then they pass through a short or long resting stage, during which time they do not feed. The pupal stage lasts from ten days to a fortnight. From numerous experiments with the Madras species it has been found that the complete life history from the egg to the imago lasts from four to five months, and that there are usually two broods during the year. In other countries the length of life history varies, and the larvae of many species hibernate during the cold weather. The larvae of the larger species and the nearly full grown stages of the smaller species feed almost exclusively on earth worms, whose body juices they suck out; this explains how gregarine cysts (*Monocystis*) are not uncommonly found in the alimentary tract of the imagines.

The larvae of the different species are very like each other, and it is often difficult to distinguish the mature larvae of the smaller flies from the young larvae of the larger species. The points to be noted are:—the abdominal markings, such as the presence or absence of striae, the character of the pseudopods, the length of the syphon tube, and the structure of the antenna. In the case of the pupa the following points should be noted:—the length of the antennal sheath, the character of the thoracic spiracle, particularly its inner margin, the length of the hairs on the abdomen, the structure of the abdominal spiracles, and the shape and size of the spines and teeth on the eighth segment.

There should be no difficulty in finding the larvae of any of the Tabanidae in a locality in which the flies are common. It is, as a rule, only necessary to collect the wet mud from the margin of the nearest patch of water and place it in a bucket or kerosine oil tin. Water is then added in sufficient quantity to form a thin fluid. The larvae of the larger species, if they have air sacs, will at once float up to the surface of the water. The muddy water should now be thoroughly stirred up and then poured through a large circular sieve with a fairly course mesh; if there are any larvae in the mud they will be caught by the sieve. This is the quickest way of finding these larvae, and in a locality where they are plentiful many hundreds may be collected in a short time; it should be remembered that the mature stages of some species travel long distances away from the edge of the water over which the eggs were laid, and may be found in almost dry mud. The pupae are always found at some distance from the water, just below the surface of the earth; they are difficult to recognize. Digging up mud from the edge of a pond or river with a stick, and turning it over bit by bit is tedious and never gives such good results.

Breeding Technique

The student of medical entomology owes much to Professor Hine's pioneer work on the breeding of the American Tabanidae. Since his papers were published work of a similar nature has been carried out in the Soudan by King, and Howlett has bred some species at Pusa in Bengal. By using Hine's methods of rearing the immature stages in glass jars of various sizes it is possible to breed out a few flies, but large numbers cannot be raised. As the larvae very soon begin to destroy each other, hundreds of bottles, each to contain a single larva, are necessary; the work then becomes cumbersome. It will also be found that the young larvae when separated into the jars are apt to die. The jars are, however, of considerable value when the larvae are about three-quarters grown, or when they are about to pupate; at this stage they do not require so much attention, as they are much hardier. The use of jars at an early stage of the experiments has, therefore, been abandoned and instead large trays have been utilized with considerable success. The method of constructing and using these trays will now be described.

A sheet of galvanized iron seven feet long is made into a tray about six inches deep by turning up the sides and soldering up the corners; this can be done by any tinsmith. The tray is then tested to see that it is water tight. It can be used for rearing the larvae by filling it with sand and mud sloped off so as to simulate as near as possible the side of a stream or pond (Plate XLIV, fig. 2). Different kinds of water plants are now planted in the mud and the tray is about three-quarters filled with fresh water, preferably from a stream; in this way about a foot or more of the mud is left uncovered. The water must be changed every ten days, and in order to accomplish this a hole should be bored in the bottom of the tray near one corner; a well-fitting cork will prevent the water from escaping. It is important to remember that if the mud used in filling the tray is brought from the side of a river or pond, it may already contain some large tabanid larvae; if small larvae are put into the tray they will soon disappear, for as noted above tabanid larvae are fond of eating their own kind. The mud should first be mixed with water and then passed through a sieve, and in this way all large larvae will be removed.

The tray described above can be readily converted into a cage of any height by making a framework of stout wire, which is soldered at intervals to the outer sides. Mosquito netting is then fitted over this and tied securely round the bottom (Plate XLIV, fig. 3). The cage should be placed on a table, the legs of which are standing in large tins of water; it is well to place the table away from the wall, and if possible in an eastern situation so that it gets a few hours of sunlight in the morning. Great care should be taken to see that the net is properly secured round the bottom of the tray; spiders will find their way into the cage, and it is more than annoying to find a special fly in the clutches of one of these creatures. For the smaller species of tabanid such a large tray is unnecessary, and a piece of galvanized iron seven feet long will make two smaller cages (Plate XLIV, figs. 1 and 4).

These cages are suitable not only for breeding tabanids, but also for keeping muscids in captivity and for feeding experiments with mosquitoes. Tabanids may be kept alive in these cages for at least three weeks if they are regularly fed.

If caught specimens of tabanids are placed in suitable cages, it will be found that many of them will lay their eggs, especially if they are taken out in large test tubes every three or four days and fed on some animal, preferably a cow.

When an egg mass has been obtained the object on which it is fixed should be taken to the laboratory and placed in a small dish of water, carefully protecting it from the attacks of ants. As soon as the larvae hatch out they should be transferred to one of the trays prepared as described above. They should on no account be picked up with forceps, but drawn up into a glass pipette of suitable bore; in this way they can be easily counted. About fifty at most should be placed in each tray, as if they are well scattered there is less chance of their destroying each other. If the water contains weeds and surface plants, the young larvae will find small crustaceans and similar forms of life on which to feed; later the tray should be well stocked with earth worms of all sizes, the smaller ones being very suitable for the young larvae.

The great advantage of rearing the larvae in these trays is that they require little or no attention except the regular changing of the water, the addition of fresh earth worms about every ten days, and the removal of dead weeds, or any other decaying matter which is likely to render the water very foul. If fifty larvae are placed in each tray, and they are well scattered, about one-fifth will reach maturity. At this stage they remain in a resting condition without feeding, and should be removed from the tray and placed singly in the small jam jars (Plate XLIV, fig. 5); each jar should have a good screw top, well perforated with holes just small enough to prevent the larva from getting out. The jar should contain sufficient moist mud to enable the larva to bury itself; the mud should be changed once a week. The removal of the old mud is accomplished by filling the jar about half full of water, and stirring up the mixture with a glass rod until it is sufficiently fluid; it is then turned out over a coarse sieve, which catches the larva but permits the fluid to pass through. The larvae should not be picked up with forceps, and it is well not to touch them with the fingers, as they are capable of inflicting a sharp bite with their powerful mandibles.

In due course the larvae pupate, and are then found just at the surface of the mud and almost completely covered, at most their dorsal surfaces being exposed. It will be remembered that the imago emerges out of the pupal case through a T-shaped slit on the dorsal surface of the thorax, and the pupa lies in such a position that this can be accomplished without any accident. The pupae should be removed from the jars in the same way as the larvae, and placed in small holes in moist mud in one of the cages, which is covered with a good net. If the pupa is held by its anterior end and the last abdominal segment inserted just in the hole, it will soon wriggle itself into the desired position. A little flag with all the data relating to the particular pupa should be fixed in the mud close to it. The pupae should be kept under observation in order to secure the flies as they hatch out. If some of the larvae are left in the tray and allowed to pupate, the pupae will be found some distance from the water; it is not, however, advisable to leave the pupae in a tray containing larvae, as they are often killed.

Attention to all these details is very necessary, for these flies, more than any others, require careful handling, or the worker will find that though he began with 500 larvae, he will end with one or two flies. The secret of success in this work largely lies in obtaining as near as possible the natural surroundings of the larvae, and in order to do this it is essential to study the habits of the flies and to note exactly where, and under what conditions, they lay their eggs.

FAMILY LEPTIDAE

Flies of moderate or large size with elongated bristly bodies. Venation similar to that of the Tabanidae. *Antennae very variable, usually with three joints; the third may consist of a number of small segments and is with or without a terminal or dorsal arista. Empodium pulvilliform; tibiae with spurs. Larvae chiefly aquatic and as a rule predaceous.*

According to Austen there are four blood-sucking species belonging to three genera. Williston states that one of these, *Symphormyia*, which is found in America, has the habit of sucking blood like the Tabanidae. Its first antennal joint is thickened and elongated, and the third segment is reniform in shape; the hind tibiae have a single spur, and the anal cell is open as in *Tabanus*. The proboscis is short and stout.

Two of the other blood-sucking species belong to the genus *Leptis*, namely, *Leptis scolopacea* and *L. strigosa*, both of which are found in France; they appear only occasionally to suck blood. The hind tibiae of these two flies have two spurs and the third antennal segment is not reniform.

The fourth blood-sucking species belongs to the genus *Trichopalgus*, (*T. obscurus*), and is found in Chili; it is said to have a long projecting proboscis.

FAMILY PHORIDAE

Small, often minute, flies with a hunch-backed appearance. The third joint of the antenna is often large, concealing the other segments, and is spherical and often pointed, with an apical or subdorsal arista. The wings are usually large but may be small or entirely wanting. There are two strong veins extending half way to the apex of the wing, and several weaker ones running obliquely across the wing. The larvae usually live on decaying vegetation or animal matter; some live in ants nests.

Aphiochaeta ferruginea, Brunetti. **Female.** Head brownish yellow, tinged with grey; antennae pale yellow, third joint large as in most of the members of the Phoridae; arista long and minutely pubescent. The frons has four rows of four bristles. Thorax bright ferruginous or brownish yellow. Abdomen dark ferruginous or brownish yellow; sometimes it is blackish with a red tinge, altering the general appearance of the fly. It is widely distributed, and has been recorded from most parts of India, Ceylon, Burma, Malay, West Indies and Central America.

Its larva is of a yellowish colour; the anterior extremity is pointed, the posterior end is bluntly rounded off, and armed with a number of short stiff spines. The pupa, according to Austen, is buff-coloured, and of the usual boat-shape characteristic of the family; the anterior end at first tapers and then becomes abruptly truncated. The posterior extremity is blunt and has a row of minute spines.

This is one of the most important phorids, as it infests the human intestinal canal in its larval stage. Brunetti states this fly was originally sent to the Indian Museum in 1891 by Crombie with a note that it was, 'reared from eggs passed in the excrement of a European in Rangoon, eggs, grubs and flies all being voided together'.

Austen, in a paper on 'Some Dipterous Insects which cause Myiasis in Man', records some observations made by Baker which suggest that *A. ferruginea* is capable of living in the human intestine, and laying its eggs, so that the patient passes out larvae, pupae and mature flies. This is a remarkable life history, and one which, at first sight, would seem to be impossible. Austen, however, points out that another phorid belonging to the genus *Conicera* has been found in America in a human body exumed two years after burial, and that living larvae, pupae and adult flies were found together.

Recently some specimens of larvae of *A. ferruginea* from the faeces of a European at Negri Sembilan, in the Federated Malay States were sent by Mr. Jackson to the King Institute for identification; here, however, there were no adult flies seen in the faeces. The result of the invasion of the human intestine by the larvae of this fly is that they may continue to be passed out for as long as a year, with symptoms simulating those of beri beri. *Aphiochaeta ferruginea* may also cause cutaneous myiasis; Austen records an instance of this from British Honduras.

FAMILY ASILIDAE

Small or large to very large flies, always elongate and with spiny legs. The head is broad and short, and nearly always flattened and jointed to the thorax by a well marked flexible neck; both sexes are dichoptic.

These flies have been aptly named 'Robber flies' on account of their predaceous habits; they are often to be seen resting motionless on walls, stones, railings, etc., watching for their prey, which is always some insect, often a fly. They dart with great suddenness and grasp their prey with their legs and impale it with their proboscides, usually in the region of the neck. They then return to some perch and suck out its body juices.

In Madras a small species regularly preys on *Philaematomyia insignis*, when it is laying its eggs in cow dung.

Kershaw has recently described the egg laying habits of a species of asilid (*Promachus*) from the Kwantung Province of South China. The female lays her eggs, about fifty in number, in a mass on long coarse grass stalks, the bare ends of twigs, etc., about two or three feet above ground; she covers them with a thick gelatinous substance like that used by some tabanids. The larvae hatch out in six or seven days, drop to the ground and at once burrow into the earth; it is not known exactly on what they feed, but Kershaw thinks they live on subterranean coleopterous larvae.

CHAPTER IV

SECTION 1

THE ORDER DIPTERA: THE CYCLORRHAPHA

THE suborder Cyclorrhapha is divided into two primary divisions, the Aschiza and the Schizophora, as pointed out in the previous chapter. In the Aschiza are included those forms in which the frontal lunule is indistinctly seen above the base of the antennae, while the frontal suture is entirely absent; the third antennal segment is always simple, and has either a terminal or a dorsal arista; the third vein is never forked, and there are never more than three complete posterior cells. The empodium is never pulvilliform.

In the Schizophora the frontal lunule is distinct and the frontal suture always present; none of the longitudinal veins are forked, and there are never more than three posterior cells present. The antenna is three-jointed and always simple; the arista is usually plumose and placed dorsally; most of the species are bristly insects. This group is further divided into the Acalypterae and the Calypterae. In the former the squamae are small, sometimes even rudimentary; the thorax is without a complete suture, and the auxiliary vein is often small or vestigial. In the Calypterae the squamae are well developed; the thorax has a complete suture, and the auxiliary vein is always well formed throughout its course.

Altogether there are about thirty families included in the suborder Cyclorrhapha, three of which, the Syrphidae, Pipunculidae and Platypezidae, are placed in the division Aschiza; as none of the species contained in these families are of any interest to the worker they will not be referred to again. In the group Acalypterae of the Schizophora there are no blood-sucking forms, but many of the species are of interest on account of the natural parasites they may harbour; the families containing these species are dealt with below. All the blood-sucking Cyclorrhaphic Diptera, and those forms which are of special interest on account of their domestic habits, are confined to the Calypterae.

THE ACALYPTERAE

FAMILY SEPSIDAE

Small ant-like flies of a black or amber colour. Head globular in shape; proboscis and antennae short. Abdomen slender and narrowed at the base; male genitalia prominent. Subcostal or auxiliary vein distinct or united to the first vein; anal and basal cells distinct.

The Sepsidae are commonly seen in the tropics on dung of all kinds; at first sight they may be mistaken for winged ants on account of their characteristic shape, the abdomen being narrowed at the base. In India they are extremely common on cow dung and may often be seen in swarms dancing and flitting about on its surface; their irridescent wings and the quaint attitudes they assume make them very striking objects. Their larvae can, as a rule, be recovered in large numbers from the dung on which the flies are feeding, and may be recognized by the presence of two prominent spines at the posterior end. If disturbed they have the habit of inserting their mouth parts into notches on the last segment, and by suddenly releasing them propel themselves four or five inches.

In Madras two species of *Sepsis* are infected with flagellates, one with a herpetomonas and crithidia, and the other with the crithidia alone; in the Soudan, Roubaud has found another species infected with a herpetomonas. It is interesting, in view of recent controversies, to note the presence of a true crithidia in a purely dung-feeding insect.

FAMILY CORDYLURIDAE

Medium-sized grey to black flies. Head globular; both sexes dichoptic. Wings large; auxiliary vein always distinct, basal cells large and complete. Squamae small, with the upper one concealing the lower. Abdomen with more than four visible segments.

Cordylurids are common about decaying vegetable and animal matter, and especially near foul water; many of the species of *Scatophaga* may be seen on cow dung. The species are of practical interest in that they may be infected with flagellates of the genus *Herpetomonas*. The Cordyluridae may be distinguished from the Anthomyidae, many of which have the same habits, by noting that the squamae are always small in the former and the male eyes are widely separated; in the latter the squamae are large and the male eyes are much closer together.

Mackinnon has recorded *Herpetomonas muscae domesticae,* Burnett, from *Scatophaga lutaria* in England; in this case the parasite was found in the larvae as well as in the imagines.

FAMILY BORBORIDAE

Small to very small brown to black flies. Head hemispherical; antenna short with the third joint rounded; arista bare or pubescent. Subcostal vein wanting or if present indistinct. Legs long and well developed; hind metatarsi dilated and shorter than the next joint.

This family contains, in addition to others, the two genera *Borborus* and *Sphaerocera,* the species of which may be seen in swarms about dung and other refuse. In Madras, a small *Borborus,* which is very common on cow dung, is nearly always infected with a species of herpetomonas. According to Chatton, *Sphaerocera subsultans* in France is infected with a species of herpetomonas, *H. legerorum.* Another borborid belonging to the genus *Limosina, L. hirtula,* is also infected with a similar flagellate.

Breeding technique

All the above dung flies can be bred out by collecting their larvae and placing them in some fresh dung in a large tray; when about to pupate the larvae as a rule do not migrate, so that the pupae are found in the dung. If cow dung is collected in a heap under a tree and regularly replenished large numbers of sepsids and borborids will soon collect on it, and their larvae can be obtained in a few days. The pupae should be placed in a breeding jar, such as that described further on in connection with the breeding of the Muscidae; when the flies hatch out they may be fed on fresh cow dung; the larvae, as well as the imagines, should be examined for flagellates.

FAMILY DROSOPHILIDAE

Small stumpy flies usually with characteristic red eyes. Antenna with the third joint oval; arista plumose with long but scanty hairs. Abdomen short. Subcostal vein absent or indistinct; first longitudinal vein short; basal and anal cells not distinct.

The Drosophilidae are also of interest on account of the natural flagellates which some species may harbour. In all parts of the world they are common about fruit, and the fermenting refuse which collects around wine vats. Though popularly spoken of as Fruit Flies, the Drosophilidae should not be confused with the Trypetidae, the well-known fruit pests. Howlett records a species of *Drosophila* from Northern India which completes its whole life history within a week; this is, as he points out, the shortest life history yet recorded for an insect with a complete metamorphosis.

In Madras there are two species which are commonly seen hovering about ripe fruit, especially during the rainy season; both are infected with a species of herpetomonas. In France another species, *Drosophila confusa*, is commonly infected with *Crithidia drosophilae*, Chatton and Alilaire.

In order to breed these flies it is only necessary to place some bananas in a tray, and allow them to become over-ripe; the flies will soon collect on them in large numbers and deposit their eggs, which are very small and have two long filamentous processes. If the fruit is not disturbed the pupae will be found in large numbers collected on the outside of the bananas, and along the sides of the tray. As in the case of the dung flies the pupae should be placed in the breeding jar and the imagines fed on fruit; the larvae should always be examined for the flagellates.

THE CALYPTERAE

FAMILY ANTHOMYIDAE

Small to medium-sized flies in general appearance resembling those of the genus Musca; greyish or brownish black in colour, rarely metallic. Male less dichoptic than the female. Antenna of the muscid type; arista either plumose or bare. First posterior cell widely open. Abdomen composed of four or five visible segments, rarely armed with bristles. Squamae well developed.

This family contains the genus *Homalomyia* (*Fannia*), the species of which have domestic habits and regularly enter human habitations. *H. canicularis* is the best-known example, and is popularly spoken of as the 'Lesser house fly'; its larvae have been recorded from the human intestine. The larvae of the majority of the Anthomyidae are vegetable feeders, and many are destructive to garden produce. Others again breed in dung and the decomposing bodies of animals; these forms are usually infected with natural flagellates. Mackinnon records *Herpetomonas muscæ domesticae* from the larva of *Homalomyia corvina* from cow dung. In Madras there are several of these dung-frequenting anthomyids which are also infected with flagellates; one in particular can be caught in large numbers by placing some decomposing meat in the open.

FAMILY TACHINIDAE

Small to large, bristly flies with thick-set bodies. Antenna of the muscid type; arista entirely bare. Proboscis either short or long. Abdomen composed of four or five visible segments armed with lateral and terminal bristles. First posterior cell either narrowed or closed. Squamae well developed. Larvae parasites of other insects. Adult flies flower feeders.

At the present time this family contains nearly 200 genera, about 180 of which are found in North America; many of them bear a superficial resemblance to the Sarcophagidae (see below), but can be distinguished by the bare arista, the well-developed squamae and the closed or narrowed first posterior cell. The mature insects live on the juices of plants and flowers, and are usually found in places frequented by the hosts which they parasitize. The larvae of the Hymenoptera and Lepidoptera are their usual hosts, but some parasitize those of the Coleoptera, Orthoptera, Hemiptera and even Diptera. In America their breeding habits have been carefully studied, and several species have been used in checking other injurious insects, particularly certain species of moth, but it must be admitted with very little success. The various methods employed by the female flies in parasitizing their hosts are described in the case of several species by Townsend in a paper entitled, 'A record of results from rearing and dissections of Tachinidae'; the worker who is interested in this subject should consult this valuable paper.

FAMILY SARCOPHAGIDAE

Medium-sized to large thick-set flies. Front broad in the female, somewhat narrower in the male. Arista plumose to the middle or a little beyond it, the distal portion bare. Abdomen composed of four visible segments; bristles as a rule confined to the distal portion, but sometimes present on the margins of the second and third segments. First posterior cell narrowed or closed. External genitalia of male prominent.

The Sarcophagidae, or 'Flesh flies' as they are commonly called, may be seen about decaying animal and vegetable matter; in India they frequent latrines and night soil trenches. Although the family contains only a few genera, the species are numerous and very difficult to distinguish. Their larvae feed on animal and vegetable matter, or live as parasites in sores, causing dermal myiasis, and in the nasal cavities of man and animals. In Gujarat it is not uncommon to see large sores on the scalp full of the larvae of a species of *Sarcophaga.* A case of nasal myiasis, in which numbers of the larvae of a species of *Sarcophaga* were recovered by nasal douching, has been recorded by Patterson from Assam. As so little is known regarding this habit among the Sarcophagidae it is not possible to say whether it is one of the regular methods of reproduction or not. In Madras the larvae of several species are found in human faeces and in the dead bodies of animals ; in the tropics food of this nature is abundant everywhere.

The flies of the genus *Sarcophaga* are larviparous, and Fabre, in his delightful account of the habits of the Blow Fly (*Calliphora erythrocephala*), points out that the female *S. carnaria* will deposit her larvae on a piece of meat from a height of twenty-six inches, thus showing that the common wire dish cover or meat safe affords little or no protection, for she can drop her larvae through the meshes.

The larva of *Sarcophaga* is amphineustic, pointed anteriorly and rounded posteriorly ; the segments are differentiated by large transverse swellings, each provided with a circlet of spines. The posterior stigmata are concealed in a depression in the last segment, and there are prominent bifid anal swellings. The puparium is reddish brown and ovoid in shape.

A large species of *Sarcophaga* in Madras is nearly always infected with *Herpetomonas sarcophagae*, Prowazek ; according to Roubaud *Sarcophaga nurus* in the Congo is infected with *Herpetomonas muscae domesticae*, and Swingle has recorded another species of herpetomonas, *H. lineata*, from *Scrcophaga sarraceniae* in North America.

Breeding Technique

In order to breed these flies for experimental purposes some decomposing meat should be placed in a tray in the open ; the female *Sarcophaga* is attracted to it, and when the larvae are deposited the meat should be placed in a mud enclosure (Plate XLIV, fig. 5) made as follows :—Mud and cow dung are mixed together and made into a walled enclosure one foot square and eight inches high ; while the mud is still moist a board is accurately fitted as a cover on the top, in order to keep out stray flies. The mud is allowed to dry until it becomes quite hard, and the enclosure is then ready for use. It should be built on to a table so that it can be protected from ants. The meat containing the larvae is placed in a small tin tray, which is then laid on sand at the bottom of the enclosure. Such an enclosure can be made by most natives, and is useful for breeding Muscidae. If the meat is left in a tray containing some sand on a table in the laboratory the larvae will crawl out of it when they migrate in order to pupate, and will be found scattered all over the floor of the laboratory. These larvae will even crawl out of a large glass jar. From experience it has been found that they never leave the mud enclosure, but always pupate in the sand. This enclosure has the further advantage of minimizing the smell from the decaying meat; if the latter is left in a tray or glass jar it becomes unbearable. The enclosure will be referred to again in connection with the breeding of *Musca*.

FAMILY OESTRIDAE

Medium to large flies with thick-set bodies, large heads and rudimentary mouth parts. Antenna short, three-jointed and hidden from view in the facial groove. Front wide in both sexes; eyes comparatively small. The thorax has a distinct transverse suture; the squamae are as a rule large, but may be small. Wing venation of the muscid type; the first posterior cell is either narrowly open or entirely closed.

This family consists of a comparatively small group of flies of the utmost importance to the veterinarian, and of the greatest interest to the dipterologist. They are popularly known as 'Bot flies', 'Warble flies', or 'Breeze flies'. The mature insects are as a rule found either in the open country resting on leaves, or on the ground along roads and pathways frequented by the hosts which they parasitize.

The great economic importance of the Oestridae has long been recognized, and it is not, therefore, surprising to find that their life histories were known to Linnaeus and many of the older entomologists. The best modern account of this family is that of Brauer, who unquestionably had the most profound grasp of the subject; his monograph is still the standard work on the structure and life histories of the Oestridae.

Classification of the Oestridae

Numerous attempts have been made to classify the Oestridae, first according to the structure of the larvae, and secondly according to their habits. They were formerly divided into two groups, those in which the larvae have oral hooks, and those without external mouth parts. Brauer points out that though this grouping is useful in distinguishing the full-grown larvae, it is incorrect, as *all* oestrid larvae have oral hooks when very young. It is also an unnatural classification, as no relationships exist between the two types of full-grown larvae and the perfect insects.

Clark suggested the second method of grouping the larvae, viz., to arrange them according to their habits, into *cavicolae*, *cuticolae* and *gastricolae*, but Brauer points out that this classification is also inadequate, for while the species of a genus may agree in their parasitic life histories, the larvae of different genera may have the same habits. He instances the habits of the larvae of *Hypoderma*, *Cuterebra*, *Dermatobia* and *Cephenomyia*, and points out that there is far more difference between the mature insects of one and two, than between two and three. The larvae of *Cephenomyia* live, as a rule, in the oesophagus, the *Oestrus* larvae in the frontal and nasal cavities, the *Gastrophilus* larvae in the intestinal tract, and those of *Hypoderma* in the subcutaneous cellular tissues.

The adult flies have been grouped according to the structure of the antennal bristles, into those in which they are *pectinate* (*Cuterebra* and *Dermatobia*), and those in which the bristles are *naked* (*Hypoderma*, *Gastrophilus*, *Cephenomyia*, *Cephalomyia*); the larvae of the former are found in the bodies of Rodents and Marsupials, and in Ungulates; those of the latter only in Ungulates. These groups are, however, unnatural, for the larvae of *Oestrus leporinus*, which has *naked* bristles, is parasitic in a rodent, as its name implies. Brauer considers it best to classify the larvae according to their genera, for those of each genus have a similar life history. The generic characters of the imago always afford a reliable clue to the probable life history of an unknown larva; in the case of new genera experience is the best guide in predicting the probable life history of the larva.

Williston's Key to the Genera of the Oestridae.

Imagines.

1. Mouth parts very small, vestigial; arista bare **2**
   Proboscis geniculate, inserted in a deep slit; female without extricate ovipositor; first posterior cell narrowed or closed; arista bare or plumose; facial grooves approximated below, enclosing a narrow median groove or depressed surface; squamae large **6**
2. The fourth longitudinal vein runs straight toward the border of the wing, i.e., the apical cross-vein is obsolete, and the first posterior cell is narrowed; squamae small; female ovipositor elongate; larvae in stomach and intestinal canal . **Gastrophilus.**
   The fourth vein turns forward to form the apical cross-vein, closing or narrowing the first posterior cell **3**
3. Facial grooves approximated below, leaving a narrow median groove or depression **4**
   Facial grooves remote, enclosing between them a broad, gently arcuate, shield-shaped surface; squamae large; female with elongate ovipositor; larvae hypodermatic **5**
4. First posterior cell closed and petiolate; body nearly bare . **Oestrus.**
   First posterior cell narrowly open; body pilose . . . . **Cephenomyia.**

5.	Palpi wanting	**Hypoderma.**
	Palpi small, globular	**Oedamagena.**
6.	Arista bare, short and stout; wings without stump at angle of fourth vein	**Bogeria.**
	Arista pectinate above	7
7.	Tarsi broad and flattened, hirsute; alulae large	**Cuterebra.**
	Tarsi slender, not hirsute; third joint of antennae more elongate; front prominent anteriorly; alulae of moderate size	**Dermatobia.**

Structure of Oestrid larva

The body of the Oestrid larva is composed of twelve segments, the first two of which cannot be differentiated from the cephalic ring; no head can be recognized. The anterior stigmata appear as small knobs or fissures and are partially hidden in the folds of skin (*Gastrophilus*). The posterior stigmata may be protrusile or retractile. In the mature *Gastrophilus* larva and in that of *Dermatobia* they are protected by lip-like organs on the last abdominal ring; in all the other genera they can be simply withdrawn into the preceding ring; they consist of chitinous, cresentic or reniform plates.

All the young larvae have mouth parts; in the later stages some have oral hooks while others have none. In *Hypoderma* the appearance changes after the first moult and the oral hooks and mouth parts disappear. The antennae are rudimentary, consisting of membraneous papillae. The anus is small, and is situated between the stigmal plates. The larvae moult twice during the parasitic period. In the third stage they reach their full size, change in colour, and are then ready to leave their hosts; those living in the skin drop out and pupate in the ground, while those in the various internal organs are either passed out or crawl out in order to pupate. They all feed on the juices of the host, or on the exudation which surrounds them.

Williston's Key to the Oestrid Larvae

1.	Last abdominal segment free, broadly attached	2
	Last abdominal segment (twelfth) retractile within the preceding, small and distinctly constricted	7
2.	Larvae with two pairs of chitinized jaws; that is with two outer mouth-hooklets, and two inner, straight, triangular points (Horses)	**Gastrophilus.**
	Larvae with two or no mouth hooklets	3
3.	Larvae on the median segments with dorsal, spindle-shaped tubercles; one pair of mouth hooklets present	4
	Larvae without such tubercles; one pair or no mouth hooklets present	5
4.	Antennae broadly separated; body oval, strongly convex above, flat below (Sheep)	**Oestrus.**

	Antennae approximated or contiguous; body elongated, somewhat broader in front than behind (Deer)	**Cephenomyia.**
5.	No mouth hooklets	6
	Two small mouth hooklets present (Rodents)	**Oestromyia.**
6.	Bristly covering alike above and below (Reindeer)	**Oedamagena.**
	Bristles stronger below than above (Ox, etc.)	**Hypoderma.**
7.	Larvae oval (Rodents, Marsupials)	**Cuterebra.**
	Larvae club-shaped, more slender posteriorly (Artiodactyls, Carnivora, Primates)	**Dermatobia.**

GENUS GASTROPHILUS, LEACH

This genus, the main characteristics of which are given in the above keys, contains some fourteen species distributed all over the world. Those larvae which are known live in the stomach and intestines of Equines; the adults are known popularly as ' Bot flies '. Garman gives the following key for the identification of the common species :—

KEY TO THE COMMON SPECIES OF GASTROPHILUS.

1.	Discoidal cell closed by cross-vein	2
	Discoidal cell open	**pecorum.**
2.	Wings marked with brown	**equi.**
	Wings not marked with brown	3
3.	Anterior basal cell nearly, or quite, equal to the discoidal cell in length	**nasalis.**
	Anterior basal cell markedly shorter than the discoidal cell	**haemorrhoidalis.**

Gastrophilus equi, Fabr., the bot fly of the horse, is the commonest species, and has long been familiar to farmers and veterinarians. The fly is of a brownish colour with rows of black spots on the lower borders of the abdominal segments; the wings are pale with dark transverse bands about the centre. When about to oviposit the female fly hovers near a horse with its body bent downwards and the ovipositor fully extended; it then darts suddenly on to the skin and glues an egg lightly on to the end of a hair, and then rapidly retreats to hover again until the next egg is ready to be laid. The egg is pointed at the lower end, while the upper has a well marked operculum. Osbourne, who has studied the conditions under which the eggs hatch, has found that they require some friction and moisture to enable them to do so, and that this is supplied by the horse licking its skin, or that of another horse. Hatching sometimes takes place before the tenth day after the eggs are laid, but more usually after the fourteenth day. This knowledge is of importance for it enables the horse keeper to know within what period he should destroy the eggs.

Gastrophilus haemorrhoidalis, L., the red-tailed bot fly, is another species the larvae of which are parasitic in the stomach of the horse. It is a small fly and can be recognized by the orange red tip of the abdomen ; it oviposits on the nose and lips of the horse. Its eggs are of a dark colour, and at the time they are laid contain nearly developed embryos, so that they hatch out much more quickly than those of *equi*.

Gastrophilus nasalis, L., the 'Chin fly' has much the same habits as the former species, depositing its eggs on the lips and margins of the nostrils of the horse.

GENUS OESTRUS, L.

This genus contains the well known *Oestrus ovis*, L., the bot fly or head maggot of the sheep, known to man from ancient times. It deposits its larvae in the nostrils of sheep, from which they migrate into the frontal sinuses, causing much discomfort to the animal ; when in large numbers they have been known to cause the death of the host. The larvae attach themselves by their hooks to the membraneous lining of the cavities and feed on the secretion which surrounds them ; when about to pupate they either crawl out of the nasal chambers or may be sneezed out. The pupal stage lasts about two months. The fly is found almost throughout the world.

GENUS HYPODERMA, LATRIELLE

The oestrids belonging to this genus are commonly known in America as 'Warble flies', or 'Heel flies'; they are characterized by the complete absence of palpi ; their larvae are parasites of the hides of cattle, and as such cause great loss to farmers. In a recent paper on Warble flies from Canada, Hadwen points out that the average percentage of infected hides ('grubby hides') in the provinces of New Brunswick, Quebec, Ontario, and British Columbia amounts to 32·22 per cent. This loss falls mainly on the farmer, for warbled hides are of little or no value.

The warble season in Canada, from the tanner's point of view, extends from late January to early July, the worst period being during the month of April. Hadwen found that the first larvae of *Hypoderma bovis*, de Geer, emerged from the skins on April 10th, and the last about July 2nd. The larvae were most prominent in the hides about April 10th, and had perforated the skin some time before. Hadwen states that all tanners are agreed that rough, long-haired, ill-kept animals are those which are chiefly attacked ; well-kept, sleek animals are rarely parasitised.

He thinks that this is mainly due to the fact that weakly animals cannot escape the attacks of the flies, whereas well-cared for animals resent their attentions and usually run away; such animals are usually kept in stalls during the heat of the day when the imagines are most in evidence. Warbles are less common during wet and cold weather.

Up to the time of the publication of Hadwen's paper, it was believed that *Hypoderma lineata*, Villers, was the common Warble fly of North America; it would now appear that this is not the case, *Hypoderma bovis* being the common species.

Hypoderma bovis, de Geer, is about half an inch long and in general appearance simulates a honey bee; it is a very hairy insect. On the front part of the thorax the hairs are yellow, in the middle they are black and shiny, while on the posterior part they are whitish. On the base of the abdomen the hairs are whitish yellow, in the middle portion they are dark, and at the apex orange red.

Hypoderma lineata, Villers, another North American species, is about the same size as *bovis*. The hairs on the thorax are yellowish white, reddish and brownish black; in addition there are four narrow light longitudinal lines on the thorax from which it gets its name *lineata*; a white horizontal band runs across the posterior end of the thorax. The hairs of the terminal segment of the abdomen are lemon yellow in colour.

Early stages. The egg.

The egg of *Hypoderma bovis* is about 1 mm. long and is of a yellowish white colour. It consists of two distinct parts, the egg itself and the *pedicel* or *clasping base*; the latter consists of two lips. According to Hadwen, who has studied the egg and the method by which it is laid, the pedicel end comes out of the ovipositor first; in some way or other the lips are opened and adapted to the hair close to its *root*, the sticky substance accompanying the eggs causing them to adhere to the hairs. This method of oviposition is in marked contrast to that in *Gastrophilus*, in which the egg is lightly fixed to the *end* of a hair. The eggs of *Hypoderma* are laid singly. Hadwen shows that the favourite sites for the fly to lay her eggs are in the region of the hock, the back of the knee and occasionally as high as the stifle and along the flanks. Rarely the fly will lay an egg near the jaw.

When about to oviposit the fly strikes the animal in a clumsy manner—it never planes over it as has been described by several authors—settling for a moment while it glues on its egg at the root of the hair. It is the pertinaceous way in which it repeats the process, buzzing round and striking, which makes the animal frenzied with fear and causes it to run away.

The larva

As already stated the third and last stage of the larva of *Hypoderma bovis* is found in the skin of the backs of cattle. Exactly how it reaches this situation is not clear; one thing, however, is certain, that the larvae do not burrow into the skin on hatching out of the eggs. It is at present believed that they are licked off from the skin or hairs and then make their way into the mucous membrane of the oesophagus, where they are found in their first stage. These larvae measure about 3·5 to 11·5 mm., and are armed with minute, almost invisible, rows of spines on all the segments. When this stage is completed, after about five months, the larva burrows through the muscles and eventually reaches the skin of the back, where it passes its third stage; just before leaving the skin to pupate it measures about 22 mm. in length. The larva of *lineata* has many spines on the dorsal and ventral surface of the penultimate segment, while in that of *bovis* there are no spines.

Hadwen adopted the following method of securing the larvae when they were about to leave the skin to pupate:—A piece of gauze is glued over the warble; some powdered aloes is mixed with the glue and a little dusted over the patch to prevent the cattle from licking the sores. The larvae will be found under the gauze, or on the floor of the stable, always in the morning. The pupal stage lasts from thirty to forty days.

Other bots of animals

Several bots belonging to allied genera live in the nasal cavities of animals. For instance, one species of *Cephalomyia*, Macq., (*C. maculata*,) is found in the throat and nasal cavities of the camel and buffalo in India; one species of *Rhinoestrus*, Brauer, (*R. purpureus*) lives in the nasal cavities of the horse; another *R. hippopotami*, Grünberg, in the nasal cavities of the hippopotamus; the larvae of the single species of *Pharyngobolus*, Brauer, (*P. africanus*) lives in the nasal cavities of the elephant, but the imago is unknown. The larva of the only species of *Pharyngomyia*, Schiner, (*P. picta*) lives in the pharynx of *Cervus elephas*, and is found throughout Europe. Seven species of the genus *Cephenomyia* live in the pharyngeal cavities of various kinds of deer in Europe and America.

Many rodents in America are attacked by the larvae of bot flies belonging to the genus *Cuterebra*, Clark. The common species is *C. emasculator*, Fitch, the 'Emasculating bot fly', so called on account of the habitat of its larvae which live in the scrotum of squirrels and chipmunks. The rabbit is also attacked by another species, *C. cuniculi*, Clark, which in its larval stage is found under the skin of the rabbit, causing a large tumour.

GENUS DERMATOBIA, BRAUER

The main characters of this genus are summarized in the above key; it contains one species *Dermatobia cyaniventris,* Macq. (syn. *noxialis,* Goudot).

Dermatobia cyaniventris. Head when viewed from above triangular in shape with the apex directed towards the frontal lunule. Thorax metallic blue, about as broad as it is long, with a dark median stripe, narrowest in front of the transverse suture and broadening out behind it; in addition there are two dark admedian stripes converging anteriorly towards the median stripe, which they join. There is also a dark curved band situated on each shoulder and a broader one at the sides. Abdomen ovoid, consisting of four visible segments of a metallic blue colour. Length 12 mm.

This fly is common in South America, where it is known as 'Vermacaque'; it normally causes cutaneous myiasis in animals, chiefly cattle and equines; occasionally it attacks man. The larva is of a characteristic shape, narrow and tubular at its posterior end, flask-shaped at its anterior extremity. The eggs are laid on the skin and the larvae burrow into the cellular tissue, where they form a large tumour.

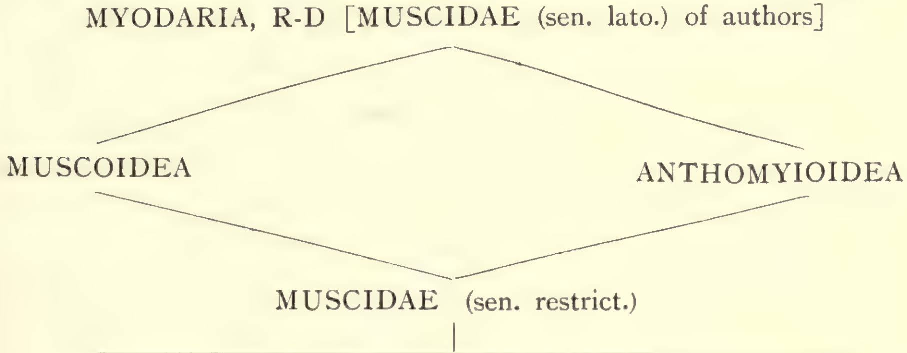
FAMILY MUSCIDAE

Small to large flies either of a bright metallic colour without thoracic markings, or greyish black with thoracic bands; they may be either bare or sparsely covered with hairs; never bristly and rarely elongate. The arista is as a rule plumose on both sides and nearly always to the extremity. The eyes, which are nearly always bare, are more or less contiguous in the male; in the female they are widely separtaed. Proboscis either long, directed forwards and armed for biting, or folded back and not armed for biting. Abdomen composed of four or more visible segments, the first fused with the second. Venation characteristic; first posterior cell closed or nearly so, except in the blood-sucking genera, in which it is open to a considerable extent; in the Glossininae the wing venation has undergone a remarkable reduction. The male genitalia are as a rule not prominent.

The blood-sucking members of the Cyclorrhapha are confined to the Muscidae. In this family there are two notorious insect pests, the house fly, *Musca domestica*, L., and the tsetse fly, *Glossina palpalis*, R-D.; the former insect, in addition to causing great annoyance, is able to contaminate food with pathogenic bacteria, and it has followed man in his migrations all over the globe; the latter transmits the parasite of Sleeping Sickness, but is fortunately localized in its distribution. The Muscidae also include several veritable pests of the domesticated animals, some of which carry dangerous parasites. Any one who has observed a horse or a cow being attacked by hundreds of blood-sucking muscids, such as *Stomoxys*, *Lyperosia* and *Philaematomyia*, will realize the extent to which these animals are worried by such insects.

Although man is not usually troubled by these smaller blood-sucking muscids, there are others, the Calliphorinae, which have the habit of depositing their eggs or larvae in his subcutaneous tissues or nostrils.

The Muscidae which concern the worker may be grouped as follows; it should be understood, however, that this table is not meant to define their exact genealogy, but rather to indicate their probable relationships.


MYODARIA, R-D [MUSCIDAE (sen. lato.) of authors]
MUSCOIDEA
ANTHOMYIOIDEA
MUSCIDAE (sen. restrict.)

CALLIPHORINAE	MUSCINAE	PHILAEMATOMYINAE	STOMOXYDINAE	GLOSSININAE
Calliphora	Musca	Philaematomyia	Stomoxys	Glossina
Lucilia			Haematobia	
Pycnosoma			Bdellolarynx	
Chrysomyia			Haematobosca	
Auchmeromyia			Stygeromyia	
Choeromyia			Lyperosia	
Ochromyia				
Bengalia				
Cordylobia				

THE CALLIPHORINAE

Medium-sized to large flies, usually of a bright metallic colour, but sometimes yellowish. Eyes bare or pubescent; cheeks bare or hairy. Arista usually plumose up to the tip, rarely bare, but sometimes pectinate. Front in male as a rule narrow, sometimes wide, as in Auchmeromyia and Bengalia. Thorax of a uniform colour usually without stripes or bands; either with or without tomentum between the bristles. Posterior dorsocentral and acrostichal bristles well developed and as a rule constant, but the former may be unequally developed. Sternopleural bristles varying in number and arranged either 0 : 1; 1 : 1 or 2 : 1. Abdomen round or ovoid, rarely elongate. Venation of the muscid type; bend of fourth vein either angular or rounded.*

In this subfamily there are about twenty genera and at least 200 species. Although none of the imagines are true blood-suckers, many of them frequent food, particularly meat when exposed for sale, and in this way they may be found to contain blood. At least one of the species belonging to the genus *Ochromyia* is predaceous in its imago stage, feeding on ants; this habit appears to be the exception rather than the rule in the *Calliphorinae*. There are, however, several grades of parasitism exhibited by the larvae of the *Calliphorinae*. As far as is known at present, all the species are oviparous, and as a rule the females deposit their eggs in decaying organic matter; in the majority of instances they prefer the dead body of some animal to any other situation in which to deposit their eggs. Some of the flies, however, will readily lay their eggs in sores and injuries on the skins of sickly animals; the larvae live on the juices surrounding them. There are several species of *Lucilia* which occasionally exhibit this habit and cause cutaneous myiasis. On the other hand, there are many species belonging to several genera in which this is the regular habit; the females are attracted by any offensive smell and even by shed blood, and will deposit their eggs in the skin and nostrils of man and animals. The last grade of parasitism, and the one which Townsend considers to be of recent origin, is well exemplified by the species of the genus *Auchmeromyia* and *Choeromyia*; their larvae are true blood-suckers and bite man and animals.

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* This method of denoting the arrangement and position of the sternopleural bristles is commonly used by Dipterologists; 0 : 1 indicates that the anterior bristle is wanting and that there is one posterior bristle, and so on.

GENUS CALLIPHORA, ROBINEAU-DESVOIDY

Medium-sized to large flies usually of a metallic colour. Posterior dorsocentral and acrostichal bristles constant and well developed. Sternopleural bristles arranged 2 : 1. Prothoracic stigmata brownish red. Base of third longitudinal vein spinulose.

This genus contains the 'Blue Bottles', or 'Blow flies', insects which are familiar to most people. All the species are of considerable size, and most of them are brightly coloured; some, however, are of a bluish to purplish tinge. They are widely distributed and are common in most parts of the world. *Calliphora erythrocephala*, Macq., and *C. vomitoria*, L., are common American and British species; the former is also found in North India. The larvae of *C. vomitoria* occasionally cause cutaneous myiasis in man and animals. As a rule, however, the larvae of the *Calliphora* are useful scavengers, as they live by destroying animal refuse. The female flies are readily attracted to the bodies of dead animals, in which they deposit their eggs. Portschinski, who has studied the life history of *C. erythrocephala* in Russia, points out that the female lays from 450 to 600 eggs, 1 mm. in length; in proportion to the size of the fly they are remarkably small.

GENUS LUCILIA, ROBINEAU-DESVOIDY

Medium-sized flies either green or bluish green. Posterior dorsocentral and acrostichal bristles constant and well developed. Sternopleural bristles arranged 2 : 1. Prothoracic stigmata black. Third longitudinal vein spinulose either at its base or throughout its length.

The flies of this genus are distributed all over the world, but the species are most numerous in tropical countries. In order to collect them it is only necessary to place a piece of meat or the body of an animal in the open, or even in a room, when several females will alight on it and immediately lay their eggs.

In South India *Lucilia serenissima*, Fabr., as a rule deposits its eggs in meat and in the dead bodies of animals, but occasionally it will oviposit in sores on the skin of sickly cattle; this often occurs during outbreaks of 'Foot and Mouth' disease in Madras. *Lucilia caesar*, L., a common European species, is also said to occasionally cause cutaneous myiasis by depositing its larvae in the skin of man and animals.

Lucilia serenissima is a common bazaar-fly in South India, and feeds side by side with *Musca nebulo* on meat exposed for sale; it is nearly always infected with *Herpetomonas luciliae*, Roubaud, and with *Rhynchoidomonas luciliae*, Patton, which is parasitic in its Malpighian tubes.

GENUS PYCNOSOMA, BRAUER AND BERGENSTAMM

Closely allied to Lucilia. Cheeks usually of a buff or orange red. Posterior dorsocentral and acrostichal bristles well developed. Sternopleural bristles only two in number, arranged 1 : 1.

The flies of this genus are the Oriental representatives of the genus *Chrysomyia*, and are by some Dipterologists included with them. They are thick-set insects and have characteristic red cheeks. In tropical countries they are abundant about night soil trenches and slaughter houses; as they frequently alight on food they may be the disseminators of disease-causing bacteria. *Pycnosoma marginale* Wied., is a common pest in the Soudan, and is widely distributed in Africa, being abundant in the Transvaal and Natal. *Pynnosoma putorium*, Wied., is common in West Africa, while *P. flaviceps*, Walk., is common in South India.

GENUS CHRYSOMYIA, FABR.

Medium-sized bright metallic flies, with three longitudinal stripes on the thorax. Thoracic bristles as a rule poorly developed and often inconstant. Sternopleural bristles three in number and arranged 2 : 1.

The flies of this genus are restricted to America and the West Indies, and the best known, *C. maceallria*, Fabr., is the 'Screw Worm fly', the larvae of which cause serious myiais in man and animals in Cuba, Brazil and other parts of Tropical America. The species are chiefly distinguished from *Pycnosoma* by the number and arrangement of the sternopleural bristles.

Chrysomyia maceallria is of a metallic blue to green colour, with three black longitudinal stripes on the thorax; the abdomen is covered with dark hairs. The legs are black and the wings transparent. It measures from 8 to 10 mm. in length.

Its larva is of a dirty white colour and consists of twelve segments, each of which is furnished with one or more circlets of spines on its upper border; the first has two, sometimes three, the second and third three each, and there are four on the other segments. The puparium is dark brown and has rudimentary spines.

Chrysomyia macellaria will lay its eggs on any part of the body which has been injured, and is readily attracted to a bleeding surface. It will also oviposit in man's ears and nostrils, especially in those of people who have offensive discharges. Freire states that the female will also deposit its eggs in decomposing carcases.

Breeding Techinque

It is important for the worker to know exactly how to breed the Blow flies, for any of the species may act as a carrier of the bacteria of cholera, typhoid and dysentery. As in the case of the Sarcophagidae, some decaying meat or the dead body of a small animal should be placed in the open in order to attract the female flies, which may either be caught with a net or allowed to lay their eggs in body of the animal. Another simple way to obtain their eggs is to catch a number of flies round a filth trench, slaughter house or from stalls in the bazaar, and to place them in large test tubes, in which some of the gravid females will lay their eggs; a small piece of meat placed at the bottom of the tube will tempt the flies to deposit their eggs. The meat containing the eggs, or the eggs themselves, should be transferred to a larger quantity of meat, which should then be placed in the mud enclosure (see page 314) as in the case of *Sarcophaga*. The larvae on hatching out grow rapidly, and when mature pass into the sand to pupate; the puparia can be collected later and placed in the fly jars as described in the case of *Musca*.

Identification of species causing myiasis

When the worker has a case of cutaneous myiasis to investigate, he should, as soon as possible, obtain several specimens of the living larvae and place them in some meat in the mud enclosure. On recovering the pupae he will be able to hatch out the fly, and will then be in a position to have it identified. This little experiment is frequently omitted, and instead, some of the larvae are preserved in alcohol, the observer being under the impression that the species can be determined by the examination of the larvae. At present practically nothing is known regarding the taxonomic characters of most of the larvae of the Calliphorinae, and it is almost impossible by examining the larvae alone to determine the species.

GENUS AUCHMEROMYIA, BRAUER AND BERGENSTAMM

Large brownish yellowish flies. Cheeks broad and prominent. Last segment of the abdomen without prominent bristles.

This genus contains the species *A. luteola*, Fabr., the larva of which is known as the 'Congo Floor Maggot', and which has the habit, unique amongst dipterous larvae, of sucking human blood. Although the fly has long been known to Dipterologists, it was not till 1904 that Dutton, Todd and Christy made the discovery that its larva does not cause cutaneous myiasis, as was supposed, but actually sucks blood, behaving in the same way as the human tick, *Ornithodorus moubata.* The above observers saw the natives in the Congo collecting the larvae by digging with a knife, or scraping with a sharp stick, in cracks and crevices in the mud floors of their huts. It was noted that they always selected those huts the occupants of which slept on the floor, and that larvae were rare in huts where raised platforms or beds were used. The flies could be seen resting motionless on the grass walls, beams and other wooden supports of the huts, but as they are of a dusky colour, simulating their surroundings, they are apt to escape observation. The natives also stated that the female flies laid their eggs on the ground, choosing particularly those places where urine had been voided.

Bionomics of A. luteola

Roubaud has recently made some observations, which are here summarized, on the habits of *A. luteola.* The adult fly always shuns light and is almost invariably found in the darkest parts of the native huts; it is very sensitive to heat and dies in the sun or when exposed to a temperature of 45° C. Roubaud states that all the species of *Auchmeromyia* are blood-feeders in their adult stages; they can, however, be kept alive for long periods on sweet liquids, but then never oviposit. In captivity *A. luteola* has two periods of oviposition, separated by about a month; a single fly has laid as many as eight-three eggs, the majority of which were deposited during the first period.

The larvae are exclusively blood-feeders, and have never been known to take any other food; they are able to resist starvation for long periods, the young larvae for three weeks, the older ones for a month or more. If fed daily their period of growth occupies about fifteen days; they moult twice, once about the second and again about the sixth day.

When buried in the earth they exhibit a remarkable sensibility to heat, becoming very active when the soil is warmed. Roubaud thinks it is this thermotropism which guides them to their hosts; they appear only to be sensitive to heat when starving, and when fed do not respond to any rise of temperature.

Structure of the larva

Dutton, Todd and Christy give a good account of the larva and its anatomy. The larva is semi-translucent, of a dirty white colour, acephalous and amphipneustic, and consists of seven segments. The first is divided by a constriction into two portions, the most anterior of which bears the mouth parts, and is capable of protrusion and retraction. At the junction of the dorsal and ventral surfaces of the larva there is a row of irregular protuberances on each of which there is a small pit and a posteriorly directed spine. At the posterior margin of each segment there is a set of three foot-pads, each covered with small backwardly directed spines, which aid the creature in its movements. The last segment is larger than the others, and bears the posterior spiracles, which are seen as three brown transverse, parallel lines. The two black mandibles protrude from the anterior segment, and are curved towards the ventral side. There are paired groups of minute spicular teeth around the mandibles, forming a sort of cupping instrument.

The intestinal canal commences as a short oesophagus, which ends in a proventriculus. A dorsal diverticulum, the food reservoir, opens into the oesophagus near its anterior end, and when the larva is replete with blood it is seen as a bright red area extending from the head to the fifth segment. The mid-gut is short, extending from the proventriculus to the junction of the Malpighian tubes with the gut. The hind-gut is considerably coiled, and occupies the greater part of the body cavity. There are two Malpighian tubes, each of which is divided into two branches. There are two salivary glands, each of which consists of a long acinus made up of large granular cells. Each gland ends in a ringed chitinous duct which unites with its fellow of the opposite side to form a common duct, the opening of which is situated near the base of the free portion of the mandible.

The *puparium* of *A. luteola* is of the usual muscid type, and of a dark brown colour. The fly is the size of a blue bottle, but is of a tawny colour ; the dorsal surface of the thorax is marked by black and brown stripes. The abdomen is characteristically marked, and has unequal segments. In the male the second segment is about one-third longer than the third, and has a black median longitudinal stripe, and another meeting it at right angles at the posterior border. In the female the second segment is two-thirds longer than the third. The legs are of a buff colour, but the first tarsal joint is black. The fly is found from Nigeria to Natal.

In a recent paper Rodhain and Bequaert state that *A. luteola* is widely distributed in the Belgian Congo and occurs all the year round. The fly probably spreads from one village to another, either in the egg or larval stage, in the dirty mats which the natives carry about with them. The fly will appear in newly constructed huts in about three weeks time.

GENUS CHOEROMYIA, ROUBAUD

Allied to Auchmeromyia; the abdomen is shorter, more tapering and has equal segments.

This genus, which has been created recently by Roubaud, contains two species whose larvae suck the blood of wart hogs and Aard-varks in the Soudan. *Choeromyia boueti*, Roubaud, is found in Niamey and Timbuctoo, where its larvae live in or near the lairs of the Aard-vark, *Orcteropus senegalensis*, Lese., and the wart hog, *Phacochaerus africana*, Cuv. The larvae of *C. boueti* resemble those of *A. luteola* and live in the damp earth in or near the lairs of these animals; the larval stage lasts fifteen days, and the pupal stage about eleven. The fly lays about fifty eggs, all in a heap, in the sand. The larvae are voracious blood-suckers, and can ingest about three times their weight of blood. Their biting apparatus appears to be similar to that of *A. luteola.*

C. choerophaga, Roubaud, is an allied species whose larvae feed on the wart hog.

GENUS OCHROMYIA, MACQUART

The flies of this genus are the nearest oriental allies to *Auchmeromyia*; with which some dipterologists group them. *O. jejune* is a common Indian species, and is usually to be seen resting on walls in Madras. It is said to feed on termites when they swarm. Howlett records having seen this fly catching ants while carrying their eggs or nymphs, and dragging the latter away from them, and sucking out their juices.

GENUS BENGALIA, ROBINEAU-DESVOIDY

Large yellowish flies. Cheeks narrow. Last segment of abdomen with prominent bristles.

Several species of *Bengalia* are known, *B. depressa* being the commonest; it is a maggot fly and causes myiasis in man and animals in many parts of Africa. According to Mennel it is widely distributed in Rhodesia, but it also ranges into British Central Africa, and Uganda. It is a large fly of a yellowish brown colour, with two dusky bands near the apex of the abdomen. Mennel states that it deposits its eggs on the hairs of animals, and on clothing, especially when hung out to dry. Fuller, on the other hand, thinks that the fly deposits its eggs chiefly on the scalp, in which situation he has seen twenty to thirty maggots. The larvae always leave their host and pupate in the ground.

GENUS CORDYLOBIA, GRUNBERG

Large brownish yellow flies resembling Auchmeromyia. Front in male narrow. Abdomen rounded and not elongate.

Three species of this essentially African genus are known, one of which is the 'Thumbu fly', *C. anthropophaga*, Grünberg, which in its larval stage ('cayor maggot') causes cutaneous myiasis in man and animals. This fly resembles *A. luteola*, but can be distinguished by the narrow front in the male and the rounded abdomen. Nothing is definitely known as to how the larvae of *anthropophaga* gain access to the human skin. Each larva forms a large swelling in the skin which has a central opening through which it breathes; like *B. depressa*, it drops out when mature, and pupates in the ground.

Rhodain and Bequaert have recently studied the habits of this fly in Katanga. They record the occurrence of cutaneous myiasis caused by its larvae in dogs, rabbits and goats; the larvae are nearly always found in the scrotum of the animals. Several cases of human cutaneous myiasis were also seen. These observers believe the fly lays its eggs on the ground in places where there is a smell of human or animal perspiration, as the tumours containing the larvae are always seen in parts of the body which come in contact with the ground. In the case of man the fly sometimes lays its eggs on clothes which are saturated with perspiration.

THE MUSCINAE

Small to medium-sized flies of a dark grey to black colour, rarely metallic. Eyes bare or pubescent. Arista either bare or plumose, sometimes pectinate. Front narrow in the male. Thorax of a grey to black colour commonly marked with two or more dark longitudinal bands. Sternopleural bristles varying in number and arranged 0:2; 1:2; 1:3 or 2:2. Venation of the muscid type. Last section of fourth vein either with a broad curvature about its middle, with a sharp or rounded angle, or curving forwards slightly beyond its middle; first posterior cell either closed or widely open.

In the subfamily Muscinae are included the non-biting Muscidae, of which there are about twelve genera. The imagines are common everywhere and exhibit varying habits. A few are true domestic insects (*Musca* and *Muscina*), and are common in and about dwelling houses and stables; the majority, however, are wild insects (*Morellia*, *Pyrellia*, etc.) The house flies (*Musca*), on account of their habits, have attracted the most attention; they are dealt with fully further on. Several species of *Morellia* occasionally come into houses; they can be recognized by their dark bluish colour and by the two broad dark bands on the thorax. Their larvae are very characteristic; they are short and have a disc-like posterior extremity on which are situated the posterior stigmata. In North America, *Morellia micans*, Macq., breeds almost entirely in human excrement. In Madras, *Morellia hortensia*, Stein, breeds in cow dung; its eggs are laid singly, and have a short curved spine. The imagines are often seen on cattle, sucking up the juices which exude from wounds and bites inflicted by biting flies. It is interesting to note that this species and another from Kodaikanal, South India, have somewhat strongly developed prestomal teeth.

Muscina stabulans, a common stable fly, is found throughout Europe and North America; it breeds in dung, and in decaying animal and vegetable matter. The species of *Pyrellia* and *Pseudopyrellia* usually breed in cow dung, though some of the former oviposit in the bodies of animals.

Genus Musca, L.

Small or moderately large insects of a greyish to dull black colour, but never metallic. The eyes in the male are contiguous or nearly so, the frons being about one-fifth the total width of the head; in the female they are widely separated, the frons being about one-third the total width of the head. The palpi are cylindrical, and slightly narrowed towards their bases. The proboscis is retractile and can be tucked away under the head, the usual position when the fly is not feeding. The thorax is nearly always marked with four narrow to broad longitudinal stripes though sometimes there are only two. Thoracic chaetotaxy (macrochaetae) as follows:—Humeral, 3; post-humeral, 1; notopleural, 2; presutural, 1; supra-alar, 1; intra-alar, 1; post-alar, 3; dorsocentral, 6 to 8, two to three in front of the suture and three to four behind it; acrostichal 1 to 3; mesopleural 6, the distance between the first and second being much greater than that between any other two; the first bristle is nearly always bent upwards; sternopleural bristles 3, arranged 1: 2; pteropleural bristles wanting. Wings hyaline, yellowish at the border; fourth posterior vein bending up at a sharp angle, and first posterior cell almost closed. Reproduction nearly always oviparous, but may be larviparous. Larva cylindrical, posterior stigmata large and widely separated, stigmal slits narrow and coiled; puparium yellowish white or olive grey to mahogany brown.

For practical purposes the genus *Musca* may be divided into two groups as follows:—

GROUP 1. The non-blood-sucking species, including all the house flies.

GROUP 2. The non-biting, blood-sucking species, including those wild forms closely resembling *Musca domestica.*

GROUP 1. THE NON-BLOOD-SUCKING SPECIES OF MUSCA

To this group belong those species of *Musca* which are domestic insects, living on all kinds of human and animal food, and on filth and garbage of every description. They come into houses and settle on food, cooked or uncooked, and on being driven away seek nourishment either from horse manure, cow dung or human excrement. They worry man especially when he has sores or foul discharges, and the reader if he has been in an Indian or African bazaar will recall the swarms of flies buzzing round some food or the sore eyes of a child. These insects are a constant source of danger to man, for they not only infect his person with bacteria, but certainly contaminate his food.

The true *Musca domestica* is found in most parts of the world. It is said to occur in North India, but is not to be found in South India. There is, however, no accurate information on this point, and this is perhaps mainly due to the fact that there are no simple complete descriptions of the group available for general use; the result is that most observers who have studied the species of *Musca* in their relations to disease germs have simply spoken of them as house flies; to the zoologist this term only refers to the species *Musca domestica*, L. It is of some importance to know exactly which species is being dealt with, as those which only breed in cow dung or the refuse around slaughter houses are not of so much importance as those which breed in human excrement.

The following short descriptions of *Musca domestica* and some of its allies will help the worker to identify his species.

Musca domestica, L. **Male**. Thorax, ground colour yellowish grey to dark grey, with four equally broad black longitudinal stripes; shoulders slate grey; scutellum dark grey with an indistinct broad central band. First to third segments of abdomen orange yellow with a median black longitudinal stripe, broadest on the third segment. Fourth segment with an indistinct diffuse olive grey patch about the centre, sides lemon yellow. In certain lights a shimmering white band is seen on either side of the central black stripe on the third segment, and a similar white patch at the sides of the second and third segments. Length 5·8 to 6·5 mm.

Female (Plate XLIII, fig. 1). Ground colour lighter than the male. Thorax yellowish grey, with four dark bands similar to those in the male; scutellum olive grey. Abdomen lemon yellow with darker patches; first segment with a central black longitudinal stripe. Second segment also with a central stripe, and two somewhat indistinct triangular brown bands at the sides; the intervening areas are silvery grey and rectangular in shape. Third segment with markings very similar to those of the second, the lateral bands narrower and pointed towards their anterior ends; fourth segment olive grey, with two narrow converging lateral brown bands. Length 6·5 to 7·5 mm.

Musca nebulo, Fabr. **Male.** Thorax, ground colour dark grey to bluish grey with four black longitudinal stripes; scutellum dark grey. Abdomen yellowish throughout with a somewhat narrow black central longitudinal stripe; fourth segment with a small indistinct olive grey patch at its centre. Length 5 to 5·5 mm.

Taken as a whole the male *nebulo* is considerably smaller and darker than the male *domestica*; the thoracic bands are narrower, and the fourth abdominal segment is much lighter in colour.

Female (Plate XLIII, fig. 2). Thorax, ground colour yellowish grey, with four clove brown longitudinal stripes; scutellum light grey. Abdomen yellow, with a black median longitudinal stripe on the second and third segments, and an incomplete stripe on the first and fourth; lateral borders of second and third segments with a faint brown stripe, and shimmering patches at the sides. Length 5 to 6 mm.

Musca nebulo is the common house fly of South India, and breeds in night soil trenches, but can be easily reared in horse dung, and in the contents of the intestines of goats, which are to be found collected outside slaughter houses in India. Its puparium is of a dark mahogany colour. It is probably much more widely distributed in India than is at present believed; it occurs in Bombay, and in parts of Gujarat.

Musca sp. incert. **Male.** Frons very narrow, much narrower than that of the male *nebulo*. Thorax, ground colour dark grey to bluish grey, with four black longitudinal stripes, broader than those of *nebulo*; scutellum black in the centre, and greyish at the sides. Abdomen dark orange with a broad black central longitudinal stripe on the second to the fourth segments inclusive, narrowest on the last; on each side of this median band there is a well-defined silvery stripe, and two similar

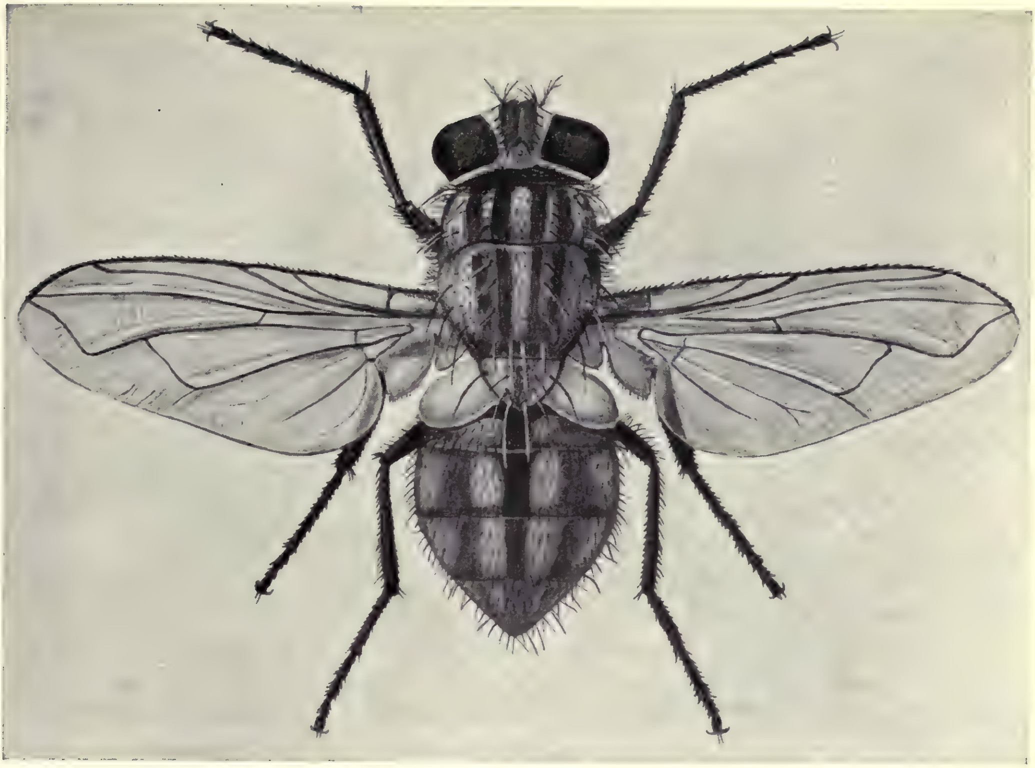

Fig. 1. Musca domestica, ♀. × 10.

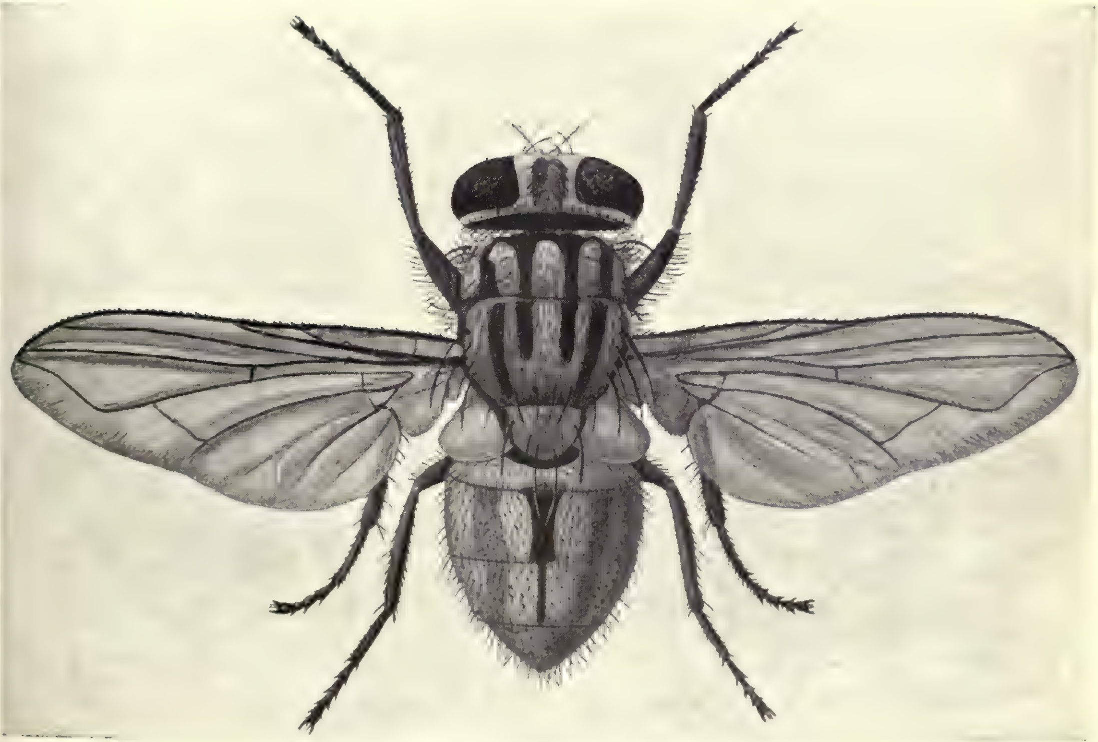

Fig. 2. Musca nebulo, ♀. × 10.

white patches at the lateral borders of the segments. Length 5·6 to 6·5 mm.

Female. Yellowish to olive grey, and quite unlike the male. Thorax, ground colour yellowish grey, sometimes appearing silvery grey, with the usual four longitudinal stripes; scutellum olive grey. Abdomen olive green with a general chequered appearance; first segment brownish grey in the centre, and olive grey at the sides, with a somewhat diffuse dark brown central longitudinal stripe, and with rectangular shimmering white bands at each side, and an indistinct lateral brown band; third segment with markings similar to those of the second, except that the central black band does not reach the lower border; fourth segment with an olive grey central patch; all the segments except the first have white borders.

After due consideration, it has been decided for the present to leave this species of *Musca* unnamed, as it is not possible to say whether it has already been described or not. It is a common house fly in Madras, and has also been seen in Bombay and Gujarat. It usually breeds in the refuse around Indian slaughter houses, and in horse dung; in Bombay large numbers of its larvae were found in a garden in rose pots which had been filled with horse manure.

This *Musca* can be distinguished from the other Indian species by the narrow front in the male and by the characteristic lateral silvery band on the abdomen. It is very difficult to distinguish the female from that of *nebulo*.

Musca enteniata, Bigot. Hewitt gives the following translation of Bigot's description of this species:—'Front very narrow, the eyes 'however separated. Antennae and palpi black; face and cheeks white; 'thorax black with three broad grey longitudinal bands; sides grey; scu- 'tellum black with two similar grey bands; halteres of a pale yellowish 'colour; abdomen fawn coloured, with a dorsal black band, and sometimes 'with light patches; legs black; wings hyaline; fourth long vein turning 'up at a slightly rounded angle, then becoming a little concave; second 'transverse vein (extreme) nearly perpendicular, and with two slight 'sinuosities, joining the fourth vein at an equal distance from the bend 'and the first transverse vein. Length 4 to 5 mm.'

The above description is very inadequate and would apply equally well to *nebulo*. After comparing some specimens from the Indian Museum, provisionally named *enteniata* by Dr. Annandale, with many specimens of *nebulo* it was found that no reliable distinguishing characters could be detected between the two. It is very probable that one or other of these names will in time have to be dropped.

Smith records *enteniata* from Benares, the specimens being identified by Austen, and states that it breeds in human excrement, and in cow dung cakes. It is also said to occur in Suez, Aden (Hewitt), and Khartoum (Balfour).

Musca domestica, sub-species *determinata*, Walker. This species, from the East Indies, is described by Walker as follows:—'Black, with a 'hoary covering; frontalia broad, black, narrower towards the feelers; 'eyes bare; palpi and feelers black; chest with four black stripes; abdomen 'cinerous, with a large tawny spot on each side at the base; legs black; 'wings slightly grey, with a tawny tinge at the base; prebrachial vein (fourth 'longitudinal) forming a very obtuse angle at its flexure, very slightly 'bent inward from thence to the tip; lower cross-vein almost straight; 'alulae whitish, with pale yellow borders; halteres tawny.'

Aldridge states that at certain seasons in Meerut it is present in enormous numbers, and Dwyer records it from Mhow. Smith found this species in a military hospital ward at Benares. It is also said to occur in Deesa, and in the Kangra valley; Hewitt records it from Aden. It breeds in night soil.

Musca angustifrons, Thomson. **Male.** Front narrow; ground colour of thorax slate grey, with two very broad black stripes tailing off at the lower border of the thorax; a broad light grey stripe running down the centre of the thorax; scutellum grey with a black apex. Abdomen olive grey with a median black stripe on the first three segments; the first segment is often entirely black or black at the sides; the second segment has a well-marked broad clove brown lateral stripe, and light patches at the sides; the fourth often has a dark median stripe which is only seen in certain lights, and two shimmering lateral patches. Length 6 to 6·5 mm.

Female. Front wide; thorax grey, with two moderately broad black admedian stripes, broadening out at the suture, where they are joined by a narrow external stripe. Abdomen with first segment dark; second with a narrow median black stripe, lateral brown bands and light patches at the sides; third segment the same except that the brown bands are narrower; fourth segment with two admedian brown bands, and light patches at the sides. Length 6 mm.

This species is widely distributed along the North African coast as well as in other parts of Africa. It is common throughout South India and occurs in parts of Bombay and Gujarat. Its habits in Madras are worth noting, for in addition to being a house and bazaar fly, it is also frequently seen on cattle, sucking up the blood which exudes from the bites of other flies, such as *Philaematomyia insignis.* It breeds in cow dung.

Early Stages of Musca (Plate XLVI)

The eggs of *Musca domestica* and its allies measure from ·8 to 1 mm. in length (Plate XLVI, fig. 1). They are of a creamy white colour, cylindrical in shape, with one end broader than the other; the dorsal surface has two curved rib-like thickenings. The *larva* (Plate XLVI, fig. 10) hatches out in from twelve to twenty-four hours according to the temperature. It measures when mature from 10 to 12 mm. in length and consists of about twelve segments, but the exact number is a matter of dispute. The second segment has at each postero-lateral border a fan-shaped structure, the anterior spiracle, which consists of from five to eight papillae; the number of these papillae varies in the different species and is useful in distinguishing the different larvae. The posterior spiracles are situated on the posterior end of the last segment. They are dark brown D-shaped structures, consisting of a chitinous ring enclosing three stigmatic slits. The larva passes through three stages or instars, shedding its skin each time. After each change the posterior stigmata become larger; at first they are small and have a single slit; at the next change there are two slits and in the last stage the slits become long and convoluted. Between the third and fourth day or even longer, according to the time of the year, the larva arrives at maturity, when it assumes a creamy white colour, due to the large amount of fat body which has been accumulated. It then slowly contracts, the outer skin at the same time hardening, until it becomes about half its original size. The *puparium* is first of a creamy yellow colour, but soon changes to a dark mahogany brown (Plate XLVI, fig. 11); the posterior spiracles are now seen as two flat projecting tubercles, at the broader and posterior end. The fly emerges about the sixth or seventh day after the egg is laid.

As the fly is about to leave the puparium, it splits off a circular piece with the aid of its frontal or ptilinal sac, which is extruded just above the bases of the antennae. When it has completely freed itself, the fly levers its way through any obstruction by inflating and deflating the sac; it then crawls about, drawing in air into its respiratory system by the aid of muscular action, and waits till its wings have become unfolded and sufficiently hard to permit of flight.

Breeding habits

According to Howard, Newstead, Hewitt, Griffith and others, *Musca domestica* prefers horse dung to any other nidus in which to lay its eggs. It will, however, breed in human excrement, and that of poultry, in bedding and other rubbish contaminated with excrement; in decaying vegetable substances, in rotten fruit and spent hops, in waste and decomposing food stuffs, in meat or in the bodies of dead animals. Very rarely *Musca domestica* lays its eggs in cow dung. Temperature is the most important factor governing the development of its larvae; the higher it is, the quicker their growth. The nature of the food supply, moisture and fermentation are also important factors.

In most European cities *Musca domestica* rarely has access to human excrement. In the case of army camps, however, where latrines have to be improvised, and where shallow trenching of the night soil is employed, this fly may become a source of danger to the occupants of the camp; in this way Howard and others explain many of the outbreaks of typhoid fever among troops in the field.

In tropical countries suitable food for the larvae is everywhere available and all the species of *Musca* have ready access to human excrement; but if this is disposed of in such a way that the female flies have no opportunity of laying their eggs in it, there is always much other refuse which is available, rich in organic matter. *Musca enteniata* in Northern India, as well as breeding in night soil trenches, is said to lay its eggs in cow dung; this is a most unusual breeding ground for flies of this group.

There are doubtless other allied species of *Musca* which are also house flies, but at present nothing is known of their habits.

House flies as carriers of disease germs

Knowing the life histories and habits of the species of *Musca* belonging to Group I, it is not difficult to understand how they may contaminate man's food with the bacteria of cholera, summer diarrhœa, typhoid and dysentery. Such contamination may take place in one of two ways: 1. Contact of the infected proboscis, wings, legs and bodies with food. Contamination is especially likely to be brought about in this way owing to the fact that these flies are intermittent feeders, flitting about from place to place. 2. Ingestion of fæcal organisms which can live and multiply in the intestine of the fly and which are passed out later on to food. Much experimental work has been carried out recently in this direction. A short summary of the results obtained will be given here.

In 1902 Firth and Horrocks carried out a series of experiments at Netley to see whether *Musca domestica* was capable of contaminating food with typhoid bacilli. The flies were kept in a large box, and were allowed to feed on some food contaminated with cultures of *Bacillus typhosus*; various culture media in petri dishes were, at the same time, placed in the box. The plates were later removed, and incubated, and were found to be infected with the bacillus. It was also found that the wings, heads, legs and bodies of the flies, when removed with sterile forceps and placed in sterile broth, gave positive results; several other experiments were carried out along the same lines, and the authors concluded that *Musca domestica* can convey the typhoid bacillus from an infected stool to sterile petri dishes, and such contamination may take place under natural conditions.

In 1903 Ficker conducted some similar experiments in Leipzig, and found that typhoid bacilli could be recovered from *Musca domestica* twenty-three days after they had been ingested. Graham-Smith examined a large number of specimens of *Musca domestica*, *C. erythrocephala* and *C. vomitoria* for intestinal bacteria of the colon type, and found that the highest degree of infection was present in those flies which were caught near decaying animal matter, and the next highest in those caught near manure. Surface infection was two and a half times more frequent than intestinal infection. In two instances an organism giving the cultural reactions of *Bacillus dysenteriae*, Flexner, was isolated. Later this observer recorded some more experiments, as a result of which he concludes that, though non-sporing bacteria only survive a few hours on the legs and wings of flies, yet they may infect sterile agar plates for several days. This is due, according to Graham-Smith, to the fact that the fly, when it feeds, regurgitates some of the contents of its crop, in which the bacteria may survive for several days; the same holds good for the contents of the intestine, though he considers that there is no evidence to show that bacteria multiply in the intestine of the fly. These experiments were carried out with a number of bacteria, among which where *Bacillus typhosus*, *B. enteritidis*, *B. tuberculosis*, *B. diphtheriae* and the cholera vibrio. The typhoid bacillus was recovered as late as the sixth day, and the tubercle bacillus as late as the third. The diphtheria bacillus was short lived, and the cholera vibrio was recovered on the third day from the intestines of the flies.

In some later experiments Graham-Smith finds that the typhoid bacillus may remain alive in the intestines of *Musca domestica* for at least six days after acquiring the infection. The tubercle bacillus will live in the fly for ten days and the spores of *Bacillus authracis* can be recovered twenty days after they have been ingested.

Cox, Lewis and Glynn recently carried out a series of experiments on the number and varieties of bacteria carried by *Musca domestica* in sanitary and insanitary areas; they arrived at the following results:—

1. More than 450 flies were found naturally infected, and 123 strains

of bacteria were studied, with the following results:—Two were streptococci, a few staphlycocci and carcinae and two strains were of *B. pyocyaneus*. Forty-one colonies of the colon group were studied, and were found to contain *B. acidi lactici* type, *B. coli communis* type, *B. neapolitanus* type, *B. lactis aerogenes* type; one of the *Salmonella* group; one of Morgan's No. I infantile diarrhœa group; and several of the proteolitic group.

2. The number of bacteria coming from flies, which fall into and struggle in liquids, may be enormous, varying from 2,000 in five minutes to 350,000 in thirty minutes.

3. Flies caught in insanitary localities contain many more bacteria than those captured in sanitary suburban areas.

4. Flies caught in milk shops contain many more bacteria than those from other shops where food is exposed for sale.

5. Flies from the suburban areas have far less bacteria of the infantile diarrhœa group than those in the city where the disease is much more common.

Ledingham and Bacot found that pupae and imagines of *Musca domestica*, which were bred out of larvae infected with *Bacillus pyocyaneus* remained infected, although there was no chance of reinfection in the pupal or mature insect stage. In the case of the imago, the infection is at its maximum when it emerges, and it then slowly diminishes. Bacot considers that the ingestion of pathogenic germs by larvae, and their persistence through the pupal stage, as well as in the mature insect which hatches out, are worthy of serious consideration.

Later Ledingham infected the larvae of *Musca domestica* with *B. typhosus*, but he was unable to recover the bacilli either from the mature larvae, the pupae, or the flies as they hatched out. From the larvae he obtained other bacteria which had contaminated the eggs, and some of these were also found in the flies. When the ova were sterilized with lysol and the larvae which emerged then fed on *B. typhosus*, he was able to recover the bacilli from the mature larvae and from a single pupa.

In the same way Graham-Smith showed that, if the larvae of *Calliphora erythrocephala* were infected with *B. anthracis*, the bacilli could be recovered from quite a large proportion of the flies as they hatched out. He failed, however, to recover *B. typhosus*, *B. enteritidis*, *B. prodigiosus*, and the cholera vibrio from larvae infected in the same way. Nicholls has carried out similar experiments with the larvae of *Sarchophagula* (a species of Tachinid) infecting them with *B. typhosus*, *B. prodigiosus* and *Styphylococcus aureus*, and a lactose fermenting organism; he found that the bacteria rapidly disappeared from the larvae, whenever they were removed from the infected material, and none of the bacteria could be found in the pupae. From these experiments and several others carried out along the same lines, Nicholls concludes that a recently hatched fly may be considered to be sterile, and that it is not likely that flies bred in infected material will be themselves infected.

In a still more recent paper Tebbutt records a long series of experiments which he carried out in order to confirm the work of Ledingham and others. He came to the following conclusions :—

1. Pathogenic organisms such as *B. dysenteriae* (Type 'Y') cannot be recovered from pupae or imagines reared from larvae to which these organisms have been administered.

2. When the larvae have been bred from disinfected ova, and are subsequently fed on *B. dysenteriae* (Type 'Y'), this organism may be successfully recovered from the pupae and imagines in a small proportion of cases.

3. Under similar conditions *B. typhosus* was not recovered in a single case from pupae or imagines.

4. In those cases in which *B. dysenteriae* (Type 'Y') was successfully recovered from pupae, the colonies on the plate were invariably fewer than those obtained from pupae and imagines after administration to the larvae of more adaptable organisms such as '*Bac. A*' (Ledingham).

5. When organisms such as '*Bac. A*' were administered to larvae bred from disinfected ova, or non-disinfected ova contaminated with this organism, it was in many cases possible to recover the organism from pupae and imagines.

6. In none of the pupae examined, after administration to the larvae of either *B. dysenteriae* or '*Bac. A*', was it possible to recover the organism in every instance. A certain proportion of pupae in both cases proved sterile, so that the process of metamorphosis is undoubtedly accompanied by a considerable destruction of the bacteria present in the larval stage.

7. The temperature at which the larvae develop (19° to 25° C.) has probably an important bearing on the survival of the pathogenic organisms such as *Bac.* '*Y*' of dysentery, administered in association with organisms such as *Bac.* '*A*', in view of the fact that the latter grows far more luxuriantly at this temperature. Even when grown in broth at 37° C. (the optimum temperature for *Bac.* '*Y*') together with *Bac.* '*A*', the *Bac.* '*Y*' was found to form after two days only one-quarter of the total number of bacteria present in the mixed growth.

8. There was no evidence that the larval juices contained substances bacteriacidal for *Bac.* '*Y*'. The bacillus died more rapidly in normal saline solution.

9. The possibility of flies becoming infected from the presence of the pathogenic organisms in the breeding grounds of the larvae may be considered to be remote.

The above represents the results of experiments carried out in temperate climates, where *Musca domestica* seldom has opportunities of breeding in human excrement. In the tropics, on the other hand, it and its allies are always found breeding in night soil trenches, and are therefore much more likely to ingest pathogenic bacteria in their larval stages; here again the number of associated bacteria is very much greater and the chances of the pathogenic bacteria surviving in the pupae and imagines are smaller. It should be noted, however, that in the tropics, where typhoid and cholera carriers are numerous, and where the various stages of the house fly are rapidly passed through, this may be a common method of infection. Whether this is so or not, the fact remains that house flies, if they feed on infected material, such as human excrement, containing the cholera vibrio, the bacilli of dysentery and typhoid, or the various bacilli associated with infantile diarrhoea, are capable not only of carrying the germs of these diseases on their legs and proboscidies but also in their intestinal tracts, and when voiding their faeces on food they may infect it.

Breeding technique

In order to study the relation which *Musca domestica* or any of its allies may have to the transmission of pathogenic bacteria, it is necessary to be able to breed the flies in large numbers, and to keep them in captivity under as near as possible natural conditions. A simple technique, not requiring elaborate and costly apparatus, must be used so that it can be controlled with the least amount of supervision. It is also very important for the worker to know for certainty that he is dealing with the same species of *Musca* throughout his experiments.

If the worker is desirous of breeding *Musca nebulo*—and what applies to this species holds good for all the others—a number of flies should be caught in a small net around food in the bazaar shops or from a night soil trench, and at once transferred to large test tubes. In catching flies indiscriminately in this way it will be obvious that there may be more than one species of *Musca* in the tubes. It is, therefore, very necessary for the worker to decide as to how many species there are

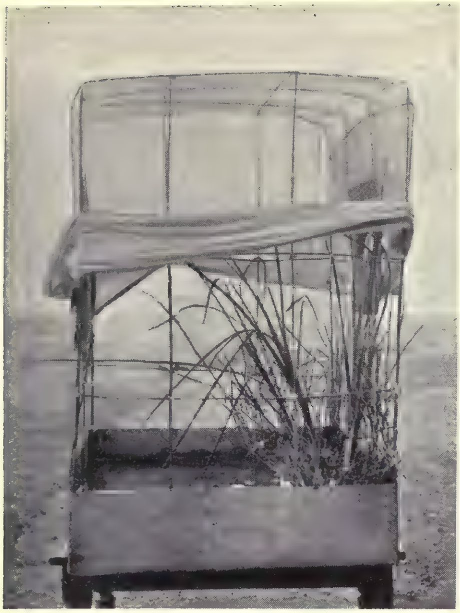

Fig. 1.

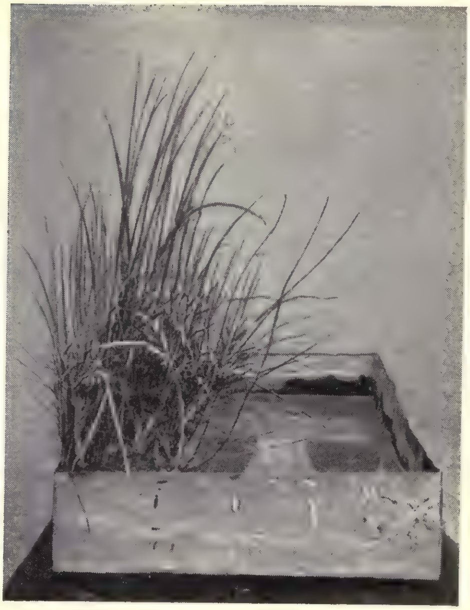

Fig. 2.

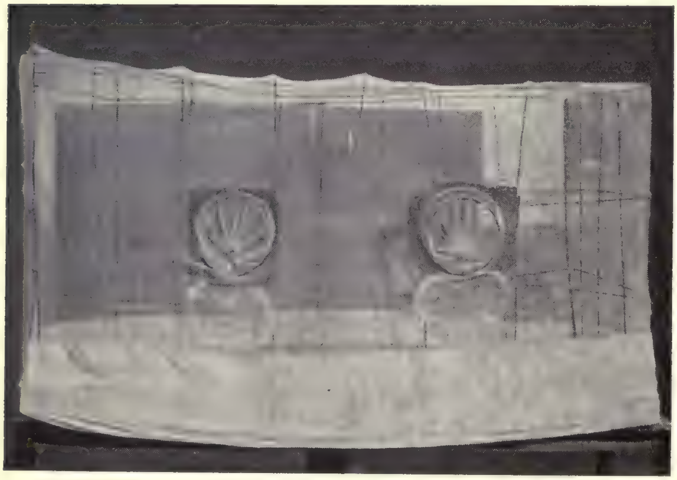

Fig. 3.

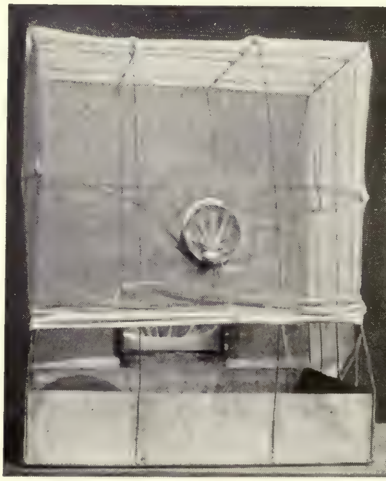

Fig. 4.

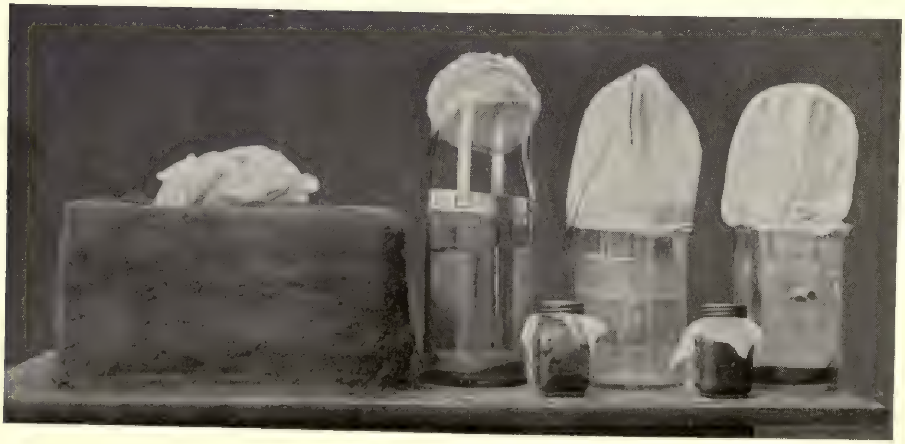

Fig. 5.

PLATE XLIV

Figure 1. Small breeding tray converted into a cage by soldering wires to the sides and enclosing it in a mosquito net. Such a cage is suitable for keeping Tabanidae in order to get them to lay eggs.

Figure 2. Large tray for rearing tabanid larvae (see page 303).

Figure 3. A large tray similar to the above converted into a cage for keeping large numbers of flies such as *Musca*, *Sarcophaga*, or *Lucilia*.

Figure 4. A smaller cage suitable for breeding *Musca*, etc.

Figure 5. The mud enclosure (see page 314) on the left; three glass jars fitted up for breeding experiments with *Musca* (see page 344); the one on the left shows the method of fixing the tin frame, the one on the right shows the food receptacle suspended in the cage. The two smaller jam jars with screw tops each contain a tabanid larva; these jars may be used for a variety of experiments. The above Photographs were taken by Dr. Gibson.

and to settle which one he is going to use for his experiments. In order to do this a preliminary experiment should be carried out.

The eggs should be washed out of the tubes with some saline solution, which is then poured, together with the eggs on to some fresh horse dung placed at the bottom of a glass jar * such as that used for preserving pathological specimens. The jar should be covered with a piece of muslin securely fastened with some tape to prevent stray flies from laying their eggs in the horse dung. It should also be remembered that if the dung is not quite fresh it may already contain the eggs of some other muscid, and if this happens much confusion will arise. It sometimes happens that fresh dung cannot be obtained, and in this case it is best to keep the dung in the jar well covered for twenty-four hours; if it contained any eggs at the time it was collected the larvae will have hatched out and can be found by disturbing the superficial layers.

As soon as the larvae hatch out of the eggs, the jar should be placed for a short time in the sun, just long enough to make the glass warm; it should then be kept in the shade and at night put inside the mud enclosure alread described (see page 314). By the fourth day the larvae will be mature, and as they will be preparing to migrate preparatory to pupating the cloth should be removed from the jar on leaving the laboratory in the evening. Several specimens of the larvae should be removed and dropped into almost boiling water, and then preserved in seventy per cent alcohol. These specimens are necessary in order to study the structure of the larva; the particular points to note, and those which prove of the greatest use in separating the species, are the number of the papillae on the anterior spiracles, and the structure of the posterior spiracles.

If the jar is placed in the enclosure and the cloth removed, the larvae will crawl out during the night and will be found next morning in the sand around and under the jar; a number will have already pupated. Several of the puparia should be collected and dropped into hot water, and then preserved either by placing them in seventy per cent alcohol in a tube or by pinning them to pieces of cork, care being taken to label the specimens. In addition some of the puparia should be placed in test tubes, one in each tube, and when the flies hatch out the pupal cases should be kept along with the imagines in the collecting box. If this preliminary experiment is carried out the worker will soon satisfy

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* The jar used by the writers is shown in Plate XLIV, fig. 5; it measures 9 inches in height and 5½ inches in diameter, and can be purchased from Messrs. Baird and Tatlock, Hatton Gardens, London.

himself as to whether he is dealing with one or more than one species of *Musca*; the imagines can be submitted later to an expert for identification.

Having cleared the ground by the above experiment the eggs of the species to be used can be obtained every day or every other day according to the number of flies required. As before the eggs should be placed on fresh horse dung, and the jar kept daily in the sun for a short time. About twenty-four hours after the larvae hatch out it is necessary to give them fresh dung and at the same time to remove that which has been used up. This is carried out by first disturbing the superficial layers of the dung with a pair of forceps, turning them over several times; as a result the larvae, which are generally at the top, at once pass down to the lower part of the dung. The upper layers can now be removed without losing any of the larvae, and fresh dung is added. In a very short time the larvae return to the fresh food, and if it is daily added to the jar in the way described growth takes place with extraordinary rapidity, and by the fourth or fifth day they will be ready to migrate preparatory to pupating. At this stage they begin to crawl up the sides of the jar, and it will be noted that there is no food visible in their alimentary tracts, an indication that they are ready to pupate. The jar should be placed in the mud enclosure as before and before leaving the laboratory the cloth cover should be removed. The larvae crawl out of the jar during the night and bury themselves in the sand, where they pupate. If the jar is not placed in the enclosure, but is left standing on a table, the larvae will force their way through the cloth covering, and, dropping on the floor, crawl into cracks or crevices in order to pupate. From extensive experience it has been found that this is the only satisfactory way of breeding *Musca nebulo* in large numbers. The larvae as they crawl out of the glass jar into the sand at the bottom of the enclosure bury themselves in it and never crawl up the mud walls of the enclosure.

When most of the larvae have pupated, the pupae should be removed, and if necessary washed, and then placed at the bottom of one of the glass jars; a tin frame made as follows is now attached to the jar (Plate XLIV, fig. 5). A long strip of tin about 1 inch in width is soldered together at the ends so as to fit closely over the mouth of the jar. At convenient distances apart four similar strips of tin are soldered to the frame, and at the other end they are soldered to a circular piece of tin which has a large hole cut out of its centre, and over which is fitted a tin lid. This upper opening is necessary in order to insert the receptacle containing the food. The tin frame is then covered with a closely fitting bag made of wide-meshed mosquito netting, which is tied with a strong tape some distance below the mouth of the jar; the upper end of the bag is closed with a purse string. As the flies hatch out of the pupae they rest on the mosquito netting.

About six hours after most of the flies have hatched out they should be given some food, either sterilized goat's spleen or sugar and water; the spleen is sterilized as follows:—It is heated when intact in a bunsen flame for about one minute, so that all bacteria which may be on the surface are destroyed. It is then placed in a sterile petri dish and cut up into small pieces with a sterile knife. One of the pieces is then passed through the flame to still further ensure its sterility as far as any surface organisms are concerned, and is placed in a receptacle which consists of an ordinary watch glass which has been sterilized and then fixed to a light tin frame; it is suspended in the glass jar containing the flies by hooking it to the netting. During hot weather it is necessary to keep the piece of spleen moist, and this is done by mixing a small quantity of sterile water or saline solution with it. Fresh spleen should be given every eight to twelve hours. The sugar and water can be put into the receptacle while it is in the cage with a glass pipette; it should be changed regularly and not allowed to ferment. Dead flies can be taken out of the jar by first removing the food receptacle and then tipping up the jar and picking them off with a pair of forceps.

In order to obtain strong healthy flies it is most important to feed the larvae regularly; if this is not done they pupate prematurely and the flies which hatch out later are short lived.

If for any reason it is not possible to obtain the eggs of a species of *Musca* in the way described above, the flies should be liberated in one of the large cages (Plate XLIV, fig. 4), at the bottom of which a quantity of fresh horse dung is placed in a tin tray; if the flies are given some food, either spleen or sugar and water, they will oviposit in the dung.

Horse dung, though an excellent food for the larvae of *Musca nebulo* has one serious disadvantage, in that it is frequently infected, at least in Madras, with the embryos of a species of *Oxyuris*, probably *O. curvula*, Rud. The larvae ingest them with their food and the worms undergo their development in the puparia, so that when the flies emerge, they are heavily infected with the adult stage. Infected flies soon die, since they are unable to feed; their proboscides are rendered rigid by the large collection of mature worms. In Madras horse dung as a food for the larvae of *Musca nebulo* had to be abandoned, and instead the contents of the intestines of freshly killed goats has been used. This material can be obtained from most Indian slaughter houses, and gives excellent results.

Another serious obstacle in these experiments is the fungus, *Empusa muscae,* which is very common in *Musca nebulo,* and may be seen in large numbers in the intestines of bazaar flies; in this case they probably become infected by ingesting the spores passed out by other flies. If the dung becomes infected with this fungus the flies fail to hatch out of the puparia.

Musca nebulo may be kept alive for as long as four weeks in one of the large cages mentioned above if certain precautions are taken. The floor of the cage should be kept clean, and this is best done by wiping it daily with a weak solution of carbolic acid. All dead flies should be removed, and the food should never be allowed to remain in the cage long enough for it to decompose or ferment.

The great advantage of using bred flies is that they can be infected either with bacteria or protozoa at any time, and the complete life history of such a parasite as *Herpetomonas muscae domesticae* can be worked out. In gauging the results of such experiments, however, it is important to remember that they are highly artificial and are carried out under most favourable conditions. Such complications as temperature and the effect of rapidly growing bacteria on the pathogenic ones should be taken into account.

House Flies which may be mistaken for Musca

It has already been pointed out that, in the case of experiments with house flies, it is important to ascertain with certainty the species which is being dealt with and not to be contented with merely stating that it is the common house fly. It is also very necessary to be quite sure that the same fly is used throughout the experiments. The various species of *Musca* belonging to Group I are extremely difficult to recognize, and for this reason specimens should be pinned and mounted in the store box with full details regarding their habits, seasonal prevalence, etc., so that they can be submitted to an expert later. It is necessary, therefore, to mention the several other kinds of flies which may be mistaken for *Musca domestica* and its allies.

All house flies do not belong to the genus *Musca* for many other kinds of Diptera are attracted by food, and in this way come under notice. There ought to be no possibility of confusing the various blue bottles with *Musca*, for they are quite characteristic. In European countries, however, there are several smaller diptera which at times come into houses and may cause confusion. One of these is the so-called 'Lesser house fly', *Homolomyia canicularis*, L., which belongs to the family Anthomyidae (see page 312). This fly is smaller and of a slenderer build than *Musca domestica.* Its thorax is of a dark grey colour, and has no distinct longitudinal stripes. If its wing is examined with a pocket lens, it will be noted that the fourth longitudinal vein, instead of bending up in its terminal portion as in the case of *Musca*, runs out to the margin of the wing parallel with the vein above it. In the resting position its wings lie closer together than in *Musca.*

Homolomyia scalaris has also been recorded from houses; it is larger but in many respects similar to *canicularis.* Occasionally *Anthomyia radicum* may be seen on window panes in houses, especially if there is any manure in the vicinity. It also has the characteristic anthomyid venation and attitudes.

The 'Stable fly', *Stomoxys calcitrans* may at times be found on window panes; it is a little larger than *Musca domestica*, but cannot be mistaken for it. Its long dark proboscis, which projects horizontally from the under surface of its head, will at once serve to distinguish it.

Muscina stabulans is another fly which is occasionally to be seen on window panes in European countries; it is not at all unlike *Musca domestica* in general appearance. It has four somewhat indistinct longitudinal stripes on the dorsum of its thorax; the wing venation differs from *Musca*, for the fourth longitudinal vein does not turn up sharply, but bends up gradually, leaving the first posterior cell widely open, as in *Stomoxys calcitrans.*

In the tropics the worker will have many species of *Musca* to deal with, and he will find considerable difficulty in recognizing them. He may find *Philaematomyia insignis* on window panes, especially if there are cattle in the vicinity; it is not a house-frequenting species like *Stomoxys calcitrans*, and only comes into rooms by accident. The several species of the non-biting, blood-sucking muscids, which will be described further on, are also extremely like *Musca domestica*; they are, however, not house flies and only very occasionally come into rooms.

Sometimes a specimen of *Morellia* or *Myospila* may be seen in a house. The former is a greyish, somewhat metallic insect, with two broad stripes on the thorax; the fourth longitudinal vein has a broad curvature near its middle, and the first posterior cell opens narrowly. *Myospila* are non-metallic species very like *Musca domestica*, but the wing venation is similar to that of *Morellia.*

It is interesting to note that in America, out of 23,087 flies caught in rooms containing exposed food, Howard counted 22,808 specimens of *Musca domestica*, or ninety-eight per cent of the total number. Of the remainder there are or were eighty-one specimens of *Homolomyia canicularis*; thirty-seven of *Muscina stabulans*; thirty-three of *Phora femorata*; eighteen of *Lucilia caesar*; fifteen of *Drosophila ampelophila*; ten of *Sarcophaga trivialis* and seven of *Calliphora erythrocephala*.

GROUP 2. NON-BITING, BLOOD-SUCKING SPECIES OF MUSCA

The species of *Musca* which belong to this group are blood-sucking by habit; they feed on the blood and serum which exudes from the bites inflicted by such flies as *Philaematomyia*, *Stomoxys*, *Bdellolarynx*, *Lyperosia*, and the *Tabanidae*; or on serum which exudes from sores on the skins of animals. It must, however, be clearly understood that these muscids are not themselves capable of piercing the skin of an animal, for their prestomal teeth are not sufficiently developed to enable them to do so.

They may often be seen in large numbers, worrying a biting fly in a very characteristic manner. They push their proboscides down beside that of the biting fly and cause it to withdraw its proboscis; if they succeed they immediately suck up the drop of blood which exudes. The male has the same habit as the female, and both can be observed flitting about from spot to spot and from one animal to another, never remaining long in one place.

It is interesting to note that these species of *Musca* appear to be common in the Philippine Islands. Mitzmain, in his paper on the Bionomics of *Stomoxys calcitrans*, evidently refers to them when he says, 'A peculiar feeding relation has been observed to exist between '*Stomoxys* and certain non-biting flies. I was curious to learn why 'such large numbers of non-biting flies were generally found in collecting 'insects from domesticated animals. When these were dissected and 'examined microscopically, mammalian blood was found to be the 'principal food constituent. My attention was attracted to the peculiar 'grouping of the ectoparasites; groups of from two to five predominated. 'On closer inspection the group was found to consist almost invariably 'of more than one species, a *Stomoxys* usually being the central figure. 'Where a *Stomoxys* was lacking, it was found that the group fed from 'a common area with the heads of the individuals in close contact. 'The food of these flies was found to be a droplet of freshly exuded 'blood, and among the blood imbibers often not an individual belonged 'to a species with a piercing mouth; they consisted principally of house

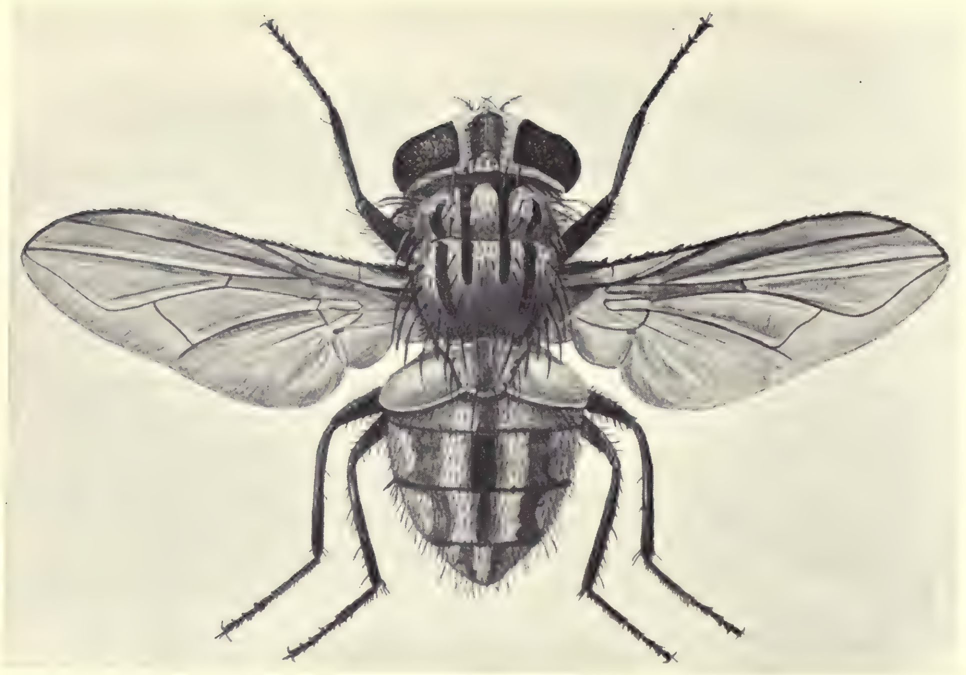

Fig. 1. Musca pattoni, ♀. × 10.

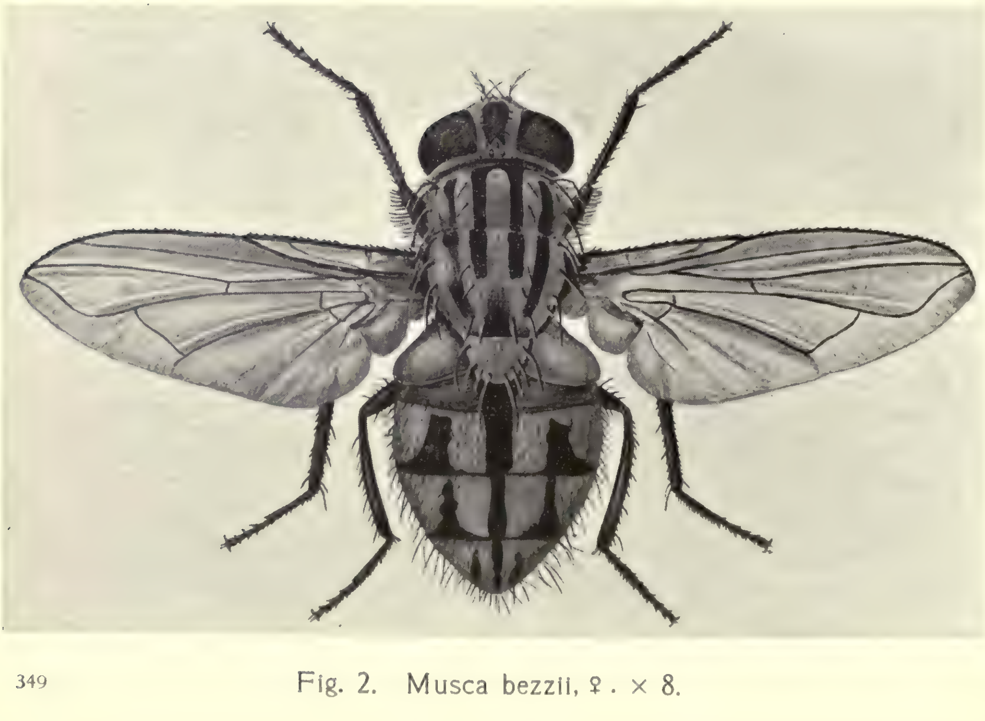

Fig. 2. Musca bezzii, ♀. × 8.

'flies'. It is obvious that this observer was not dealing with the house fly but with haematophagous muscids.

Up to the present time these muscids have attracted little or no attention, but it can be readily understood that they may act as the vectors of parasites of all kinds. In describing a recent outbreak of Trypanosomiasis (Murrina) among horses and mules in Panama, Darling pointed out that the trypanosome was, in all probability, being transmitted by flies of the genus *Musca*, which swarmed on the sick animals. A few days before death excoriated patches, which exuded trypanosome-containing serum, formed on the necks, sides and heads of the diseased animals; the flies were attracted to these sores, and as they crawled over them their legs and proboscides would naturally become infected. On passing from a sick to a healthy animal they could readily infect the latter when they insert their proboscides on the spots at which biting flies had previously sucked blood. It is quite possible that the trypanosome of Surra, for instance, is transmitted in this simple way, for there is as yet no convincing proof that any biting fly acts as the invertebrate host.

These blood-sucking muscids are of interest to the dipterologist, for they indicate the probable lines along which the true biting Muscidae have evolved; although their proboscides are structurally similar to those of Group I, it is interesting to note that in some of them the prestomal teeth are reduced in number. Short descriptions of all the known species are given here.

Musca pattoni, Austen. **Male.** Thorax, yellowish grey to bronze black, with four broad black longitudinal stripes. Abdomen ochraceous buff with silvery patches. First segment uniformly yellow with a short broad median black longitudinal stripe. Second segment with a broad triangular median black longitudinal stripe, a silvery patch on each side, and a lateral brownish patch. Third segment with markings similar to those of the second segment, except that the median longitudinal stripe is narrower. Fourth segment dark, with an extremely narrow median longitudinal stripe, and brown sides. Length 5·5 to 8·5 mm.

Female (Plate XLV, fig. 1). Thorax, yellowish grey, with four longitudinal bands, narrower and lighter in colour than in the male. Abdomen with markings similar to those of the male, but the silvery patches at the sides of the median stripe are more conspicuous, and the lateral brown bands narrower. The fourth segment is brown with a dark apex. Length 7 to 7·5 mm.

In shape and general structure the *egg* of *pattoni* (Plate XLVI, fig. 2) is similar to that of *Musca domestica*, but with a long delicate appendage (spine) at the narrow end. Each egg is laid singly in cow dung with the spine, which in the mature egg is almost black in colour, directed upwards. Length of egg 1·8 to 2 mm.; length of spine 1 mm. The *larva* is of a yellowish white colour with a slight lemon tint when mature; anterior spiracles with five papillae. The *puparium* is of a characteristic greyish white colour; the larva, contrary to the habit of the other species of this group so far as they are known, does not leave the dung to pupate; the puparia can only be recovered by breaking up the dung.

This species of *Musca* is abundant in Madras throughout the year, and according to Annandale it is also common in parts of Bengal. Its breeding habits are peculiar in that it only lays its eggs in cow dung where it is collected in heaps; it has never been seen to lay its eggs in small patches of dung in the field. It is not uncommon to see as many as eight females each depositing an egg in the same spot. The flies, for both sexes behave in the same way, are only seen on cattle and horses.

Musca gibsoni, Patton and Cragg. **Male.** Ground colour of thorax slate grey to dark grey with four broad longitudinal black stripes; in most of the specimens the stripes cannot be easily seen, as the whole thorax appears bronze black. Abdomen reddish brown with shimmering white bands. First segment black except for two horizontal yellowish brown bands at the lower border. Second segment with a broad black median longitudinal stripe, broad at the upper end and narrow towards the lower, on each side of which there is a narrow shimmering yellowish grey stripe; the remainder of the segment is reddish brown with a white patch at the lateral edge. Third segment with a narrow black median longitudinal band and a larger white patch at the edge, the markings otherwise similar to those of the second segment. The lower border of the third segment with a dark brown patch which forms a conspicuous spot. The fourth segment is dark grey to olive grey with a narrow white stripe at each side, and a lateral clove brown band. Length 5·5 to 7 mm.

Female. Thorax, yellowish with four longitudinal black stripes. Abdomen reddish yellow; first segment with a dark transverse band at the lower border as in the male. Second segment with a dark median longitudianl band narrower than that on the male; a broad yellowish grey shimmering patch at each side, and a lateral brown band. Third segment markings similar to those of the second, but all the bands are narrower. Fourth segment, centre olive grey, with two narrow lateral clove brown bands. Length 6 to 8 mm.

PLATE XLVI

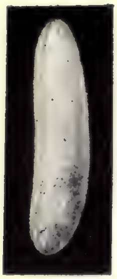
Fig. 1.

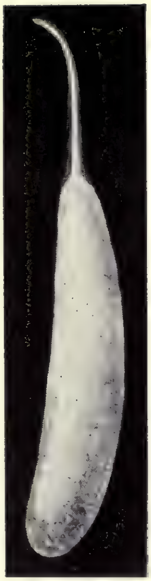
Fig. 2.

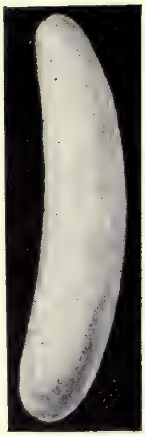
Fig. 3.

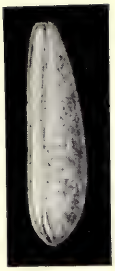
Fig. 4.

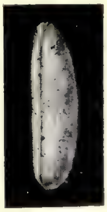
Fig. 5.

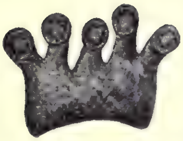
Fig. 6.

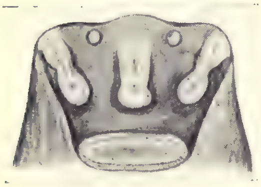
Fig. 7.

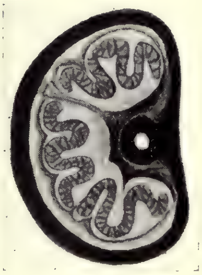
Fig. 8.

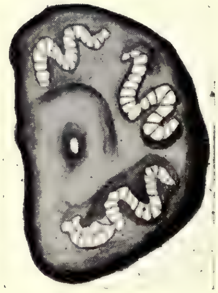
Fig. 9.

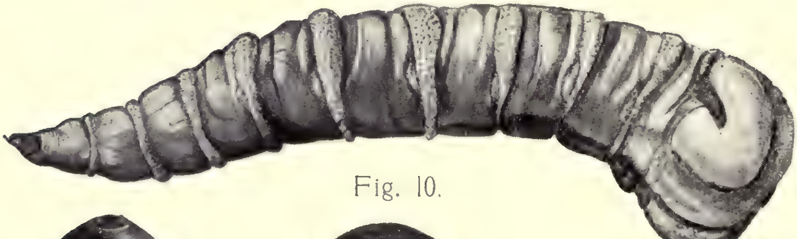
Fig. 10.

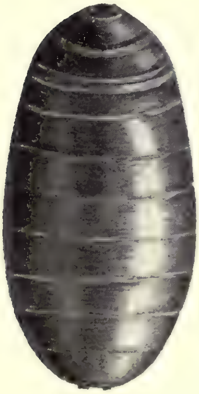
Fig. 11.

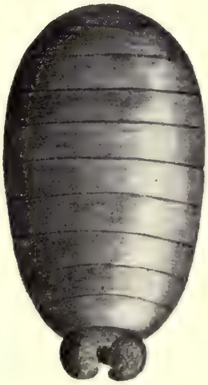
Fig. 12.

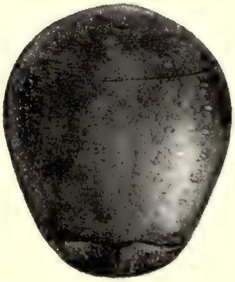
Fig. 13.

PLATE XLVI

Figure 1. Egg of *Musca nebulo.* ×16.
Figure 2. Egg of *Musca pattoni.* ×16.
Figure 3. Egg of *Philaematomyia insignis.* ×16.
Figure 4. Egg of *Stomoxys calcitrans.* ×16.
Figure 5. Egg of *Lyperosia exigua.* ×16.
Figure 6. Anterior spiracle of first larval instar of *Stomoxys calcitrans.*
Figure 7. Posterior spiracle of first larval instar of *Stomoxys calcitrans.*
Figure 8. Posterior spiracle of last larval instar of *Musca nebulo.*
Figure 9. Posterior spiracle of last larval instar of *Philaematomyia insignis.*
Figure 10. Mature larva of *Musca gibsoni.* ×6.
Figure 11. Puparium of *Musca nebulo.* ×8.
Figure 12. Puparium of *Glossina palpalis.* ×8.
Figure 13. Puparium of *Hippobosca maculata.* ×8.

The *egg* of *Musca gibsoni* is very similar in size and shape to that of *pattoni*, except that the spine is a little broader at its distal extremity; each egg is laid singly in isolated patches of cow dung. The *larva* (Plate XLVI, fig. 10) is greyish white when mature and always leaves the dung to pupate. The *puparium* is greyish white to greyish brown.

This species has so far only been found in Kodaikanal (6,000 ft.) Pulney Hills, South India, where it was extremely abundant during the month of September on cattle and horses; on one occasion over two hundred specimens were taken in two hours on a horse. It appeared to cause more annoyance to cattle and horses than did the true biting flies. The species on which it was dependent for its food were mainly *Stomoxys calcitrans* and *Bdellolarynx sanguinolentus*, which it worried in a remarkably persistent manner, as many as a dozen being frequently seen around one of these biters, endeavouring to make it withdraw its proboscis. It was often seen to be turned round on the fixed point provided by its proboscis. The biting fly appeared to resent these attacks, and to endeavour to protect itself by raising its body and vibrating its wings.

Musca convexifrons, Thomson. **Male.** Thorax, dark grey to bronze black, with four broad black longitudinal stripes. Abdomen yellowish brown; first segment with a broad black transverse stripe at its upper border, and a broad black median longitudinal band. Second segment also with a broad median longitudinal band and a silvery patch on each side of it; third segment with similar markings, but the median band is narrower. Fourth segment olive grey in the centre, often with two brown lateral bands. Length 5 to 5·5 mm.

Female. Thorax, grey to greyish black, with four narrow longitudinal bands. Abdomen reddish brown; first segment almost entirely yellow, with a narrow to broad median band. Second segment with a narrow median band; a silvery patch on either side and a reddish brown lateral band. Third segment with similar markings to the second, except that the median stripe is narrower. Fourth segment dark in the centre and at the apex, and brown at the sides. Length 5 to 5·6 mm.

The *egg* of *Musca convexifrons*, compared to that of *Musca pattoni*, is smaller and the spine is more delicate and curved. It lays its eggs in isolated patches of cow dung, placing each egg separately. The *larva* when mature is of a greyish white colour with a reddish yellow dorsum; it always leaves the dung to pupate. The *puparium* is almost pure white and is very like that of *Musca corvina*, variety *ovipara*, Portshinski.

Musca convexifrons is common throughout the year in Madras, and may be seen either on cattle sucking up blood or serum which exudes from the bites of other flies, or on patches of fresh cow dung laying its eggs. It was originally described from China, and according to Bezzi it occurs in parts of Africa.

The worker in India who encounters for the first time any one of these three species of *Musca* may find some difficulty in distinguishing them ; the following distinguishing points may be useful :—Both sexes of *pattoni* are distinctly larger than those of *gibsoni*. In the male *pattoni* the thoracic bands are broader, the thorax is lighter in colour, the longitudinal median band is narrower on the first and second abdominal segments, but broader on the third segment, than in *gibsoni* ; the silvery patches are broader, but the brown lateral bands are lighter than those of *gibsoni*. In the case of the female *pattoni*, the longitudinal band on the first segment is much narrower than that on the first segment of the female *gibsoni*. The lateral brown bands on the abdomen of *pattoni* are broader and lighter in colour, and the transverse black bands at the lower borders of the first three segments less conspicuous than those of *gibsoni*.

Convexifrons, which bears a superficial resemblance to *gibsoni*, is a distinctly smaller fly ; the male has a yellowish abdomen, while that of the female in some lights is almost uniformly reddish brown. The longitudinal band on the second segment of the female *convexifrons* is much broader than the corresponding band of *gibsoni*, and the dark lateral bands are not nearly so conspicuous as those on the latter fly.

Musca nigrithorax, Stein. **Male.** Front very narrow ; thorax black with small grey patches on the shoulders. Abdomen bright ochraceous, and without any markings.

Female. Front wide ; thorax dark with a faint indication of two black longitudinal stripes, and a dark central one. Abdomen as in male.

This handsome little fly will be recognized by its dark thorax and unbanded abdomen. In Madras it is only seen on cattle, and behaves in the same way as the other blood-sucking species described above. It also occurs in Java. It breeds in cow dung.

Musca bezzii, Patton and Cragg. **Male.** Thorax, dark grey to bronze grey, with four black longitudinal bands. Abdomen ochraceous buff with shimmering yellowish patches ; first segment with a black transverse band, not extending to the outer and lower borders. Second segment with a broad median longitudinal band, and a silvery patch on each side. Third segment with a narrower longitudinal band, a rectangular yellowish grey to silvery grey patch on either side, and a brown rectangular lateral band. Fourth segment with a narrow black median longitudinal band, and with similar bands and patches as the third segment. Length 7·5 to 8·5 mm.

Female (Plate XLV, fig. 2). Thorax, silvery grey to yellowish grey, with four narrow black longitudinal bands. Abdomen olive grey to dark grey; first segment almost entirely black. Second segment with a broad black median longitudinal band, a rectangular yellowish grey patch at each side, and a clove brown to nearly black lateral band, pointed at its upper end and broad at its lower, forming a transverse band to the segment. Third segment markings similar to those of the second, but with a narrower median longitudinal band. Fourth segment with a broad median longitudinal band, a clove brown narrow lateral stripe, and shimmering patches at sides. Length 7 to 8·5 mm.

This fly is larviparous and deposits one larva at a time in cow dung; the internal genital organs of the female are described on page 141, and figured in Plate XXX, fig. 2. The mature *larva*, which measures 10·5 to 12·5 mm. in length, is greyish white with a lemon yellow dorsum. The ***puparium*** is of a dirty grey colour, with a yellowish tinge, and is not unlike that of *Musca pattoni.*

This species is common in two Indian hill stations, Kotagiri in the Nilgheries, and Kodaikanal in the Pulneys; Professor Bezzi informs the writers that he has had specimens sent to him from Trichinopoly. It is only seen on cattle; it is closely allied to the European *Musca corvina,* variety ***vivipara,*** Portschinski.

Musca corvina, Fabr. (*ovipara,* Portschinski). **Male.** Thorax, dark grey to bronze black, with four broad black longitudinal stripes. Abdomen yellowish brown with a reddish tinge in some lights; first segment entirely black; second segment with a broad black median longitudinal stripe, broadest at its upper and lower ends, and narrow in the centre; third segment with a narrow black median stripe broadening out at its lower end. Fourth segment with a large central dark grey to olive grey patch. Length 5 to 6 mm.

Female. Thorax, light grey to dark grey, with four narrow longitudinal stripes. Abdomen olive grey; first segment dark at its upper border and centre, and light at the sides; second segment with a narrow black median longitudinal stripe, a silvery patch at each side of this, a narrow olive grey lateral band, and silvery sides. Third segment with the same markings. Fourth segment light olive grey, without any bands. Length 4·5 to 6·5 mm.

According to Portschinski, *Musca corvina ovipara* lays about twenty-four eggs, in cow dung; each egg is 1·5 mm. long and has a delicate dark spine about two-thirds its length. The *larva* passes through only two moults, the second being missed; it therefore matures rapidly, and according to Portschinski this compensates for the small number of eggs laid by the imago. In the Crimea in the early spring, and occasionally in the summer, it lays eggs in the usual way, but towards the end of spring and throughout the summer larvae were almost exclusively deposited, one at a time in cow dung; on examining these larvae Portschinski found that they were already in the third stage of development. The *puparium* is white and closely resembles that of *Musca convexifrons.*

Portschinski does not appear to have examined the internal genital organs of *Musca corvina ovipara,* so that it is not known whether they differ according to the season.

Musca corvina, Fabr. (*vivipara,* Portschinski.) This species differs from the variety *ovipara* in the following respects:—The male *vivipara* is considerably larger (7·5 to 8·5 mm.) than that of *ovipara*; the first abdominal segment is not entirely dark and there is a well-marked silvery band on the second and third segments, on each side of the median dark stripe; in addition there is a pollinose lateral band. The female *vivipara* is also larger (7 to 8 mm.) than the female *ovipara,* but the markings are very similar.

This species colsely resembles *Musca bezzii,* and Professor Bezzi informs us that its puparium is dark brown; as noted above that of *ovipara* is white. It seems very probable, as Professor Bezzi suggests, that Portschinski has confused two closely allied muscids, one oviparous and the other larviparous. Both species are common in Europe and parts of North Africa.*

Breeding technique

As all the above species of *Musca* lay their eggs in cow dung they can be bred in large numbers without difficulty. *Musca pattoni* always oviposits in dung where it is collected in heaps, and it is only necessary to watch a female laying her eggs, and later to transfer the dung to a tray, adding to it a larger quantity. The puparia will be found in the dung in about a week. *Musca gibsoni* and *Musca convexifrons* oviposit in isolated patches of cow dung, and in order to collect their larvae it is best to put some fresh cow dung in a tin tray and place it near a cow on which the flies are feeding.

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*The above descriptions of *Musca corvina ovipara* and *Musca corvina vivipara* are compiled after an examination of a long series of named specimens of both sexes sent to one of the writers by Professor Bezzi and Baron Surcouf.

In a very short time several of the females will alight on it and commence laying their eggs. When a number of eggs have been laid the tray should be taken to the laboratory and a quantity of sand placed around the dung; it should be placed in the sun for a short time each day, otherwise the dung will become covered with moulds, which are injurious to the larvae. The upper layers soon dry and become hard and keep the lower parts moist. In about three days the larvae become mature, and then pass out of the dung and bury themselves in the sand to pupate. The puparia should be collected and placed in one of the large glass jars already described.

It is sometimes possible to get the female *Musca bezzii* to deposit a larva in a test tube if some fresh cow dung is placed at the bottom.

Owing to the peculiar feeding habits of these species of *Musca* it is difficult to keep them alive for long periods; they cannot be fed in the same way as the true biting flies. *Musca pattoni* has, however, been kept alive for a week in a glass jar (see page 343) by placing large drops of blood on pieces of white paper; the flies readily sucked it up.

THE BITING MUSCIDAE

The true biting Muscidae fall naturally into three subfamilies, the Philaematomyinae, the Stomoxydinae and the Glossininae. The first of these contains the single genus *Philaematomyia*, the species of which closely resemble those of the genus *Musca*, but are distinguished from them by the presence of a cutting apparatus on the labella; the proboscis is completely retractile. In the Stomoxydinae are included the genera *Stomoxys*, *Haematobia*, *Bdellolarynx*, *Haematobosca*, *Stygeromyia* and *Lyperosia*, in which the proboscis is too long and pointed to be concealed when it is retracted. The third subfamily contains the single genus *Glossina*, the species of which have similar proboscides to those of the Stomoxydinae.

THE PHILAEMATOMYINAE

Genus Philaematomyia, Austen

Small to large flies of a yellowish grey to dark grey colour, in general appearance closely simulating the house fly. Front in male at vertex narrow, from one-sixteenth to one-sixth total width of head; width of front in female at centre from one-sixth to one-third total width of head. Antenna three-jointed and similar to that of Musca; arista with seven to *ten bristles on its upper surface, and five on its lower. Palpi cylindrical, narrowing towards their bases; proboscis completely retractile, and concealed when in the resting position; haustellum as long as or longer than the rostrum. The labial gutter is thickened, and the membraneous area between it and the mentum diminished. The discal sclerite modified in shape from that of Musca, and strongly chitinized; the prestomal teeth greatly increased in size and strength. The pseudotracheal membrane reduced in extent and in the number of the channels. Thoracic chaetotaxy (macrochaetae):—Humeral 4, the most internal bristle usually smaller than the others; post-humeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post-alar 3; dorsocentral 4 to 6, usually two to three anterior to the thoracic suture, and two to three posterior to it; acrostichal 1; mesopleural 6 to 8, the space between the first and second greater than that between any of the other two; sternopleural 3, arranged 1:2. Wings pale grey, yellowish at borders, costa with some black bristles at its base. Venation as in Musca, except that the fourth longitudinal vein bends up at a sharper angle. Reproduction oviparous, eggs large, laid, as far as is known, all together in cow dung. Larva cylindrical, closely simulating that of Musca; puparium also simulating that of Musca.*

This genus at the present time contains three species, one of which, *Philaematomyia lineata*, is not a true biting fly.

Philaematomyia lineata, Brunetti (*Pristirhynchomyia lineata*, Brunetti). Thorax, ground colour silvery to dark grey, with four moderately broad black longitudinal bands. Abdomen, first segment in male dark with yellowish sides; in female brown to black. Second segment in male with a central dark brown longitudinal stripe, sides shimmering yellow, with indistinct brown lateral bands; in female with a well-marked central longitudinal band, and the lower border edged with black. Third segment, in male, with a median brown band, and lateral brown patches; in female with a narrow dark median stripe and triangular dark patches at the sides. Fourth segment of male yellow at apex and brown at sides; in female yellowish with two indistinct dark lateral bands.

This small dark fly, which may be easily mistaken for a species of *Musca*, has been recorded from Madras and Calcutta; it is a rare fly in Madras, and is most frequently seen in the cold weather; some years it is not met with at all.

Philaematomyia gurnei, Patton and Cragg (Plate XLVII, fig. 2). Thorax, ground colour greyish black in the male, silvery to yellowish white in the female, always with four clove brown to black longitudinal bands. First segment of abdomen in male with sides and centre dark

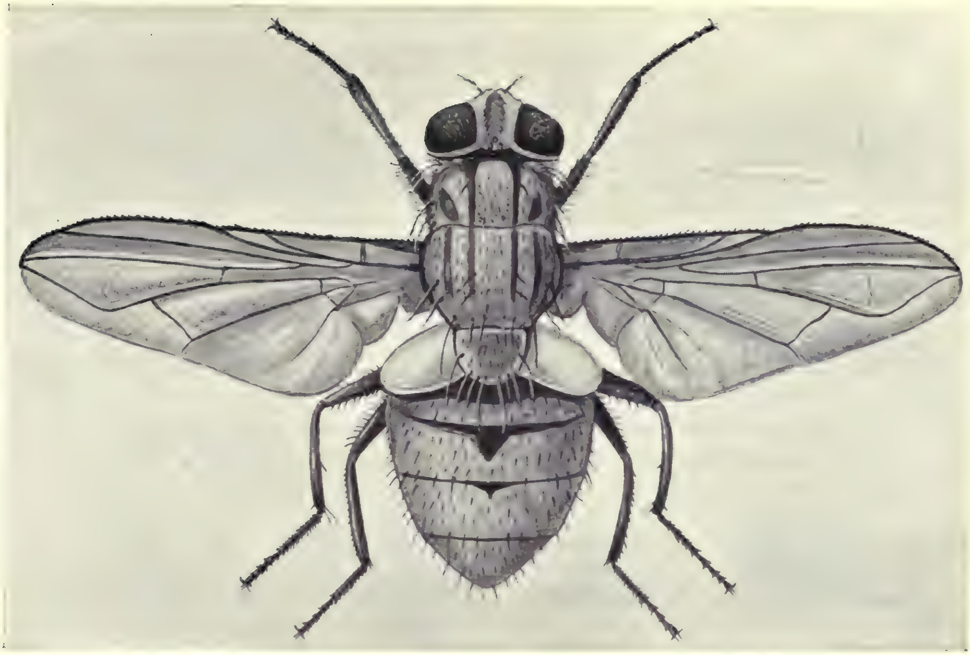

Fig. I. Philaematomyia insignis, ♀. × 8.

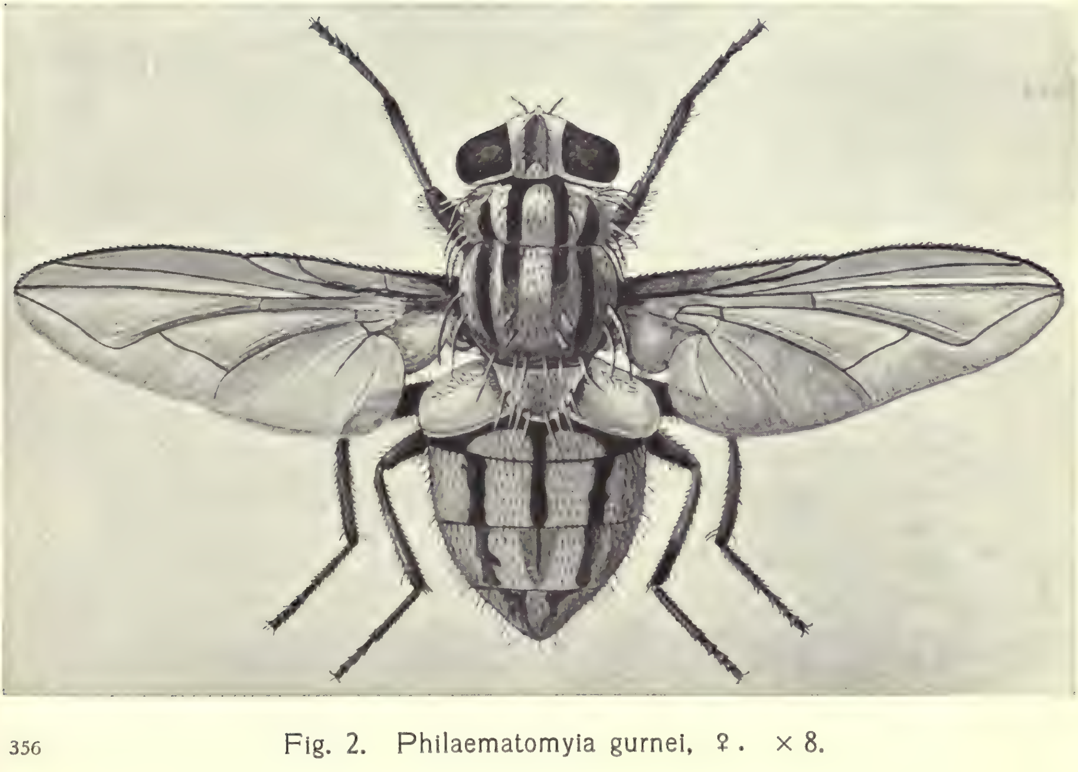

Fig. 2. Philaematomyia gurnei, ♀. × 8.

brown to black, two light patches, and with a transverse band along its lower border; in female, first segment grey with a dark longitudinal band, an oval yellowish patch on each side, and bounded with a clove brown lateral band. Second segment in male with a broad black median longitudinal stripe, a broad brown lateral band, and the intermediate areas greyish to yellowish brown; in female with a narrow dark median band, a clove brown broader lateral band, and intervening spaces and sides silvery grey. Third segment in male with a diffuse median band, otherwise markings as on the second segment; in female colour and markings similar to those of the second, except that the median band is narrower, and the rectangular areas adjacent to it much darker. Fourth segment in the male with an indistinct median stripe, a narrow brown lateral band, and sides silvery; in female with two well marked lateral brown stripes.

This species has only been found in Madras and Kodaikanal (6,000 ft.) Pulney Hills, South India; it was rare in the latter place in September, 1912, and only once seen in the former. So far it has only been taken from cattle and horses, and both sexes are voracious blood-suckers.

Philaematomyia insignis, Austen. (*Musca crassirostris*, Stein) (Plate XLVII, fig. 1.) Thorax, ground colour smoke grey to yellowish grey, with four brown longitudinal bands. First segment of abdomen in male with a dark almost black transverse patch extending to the sides, but not reaching the hind margin; in female without any distinct band, though in some specimens there is a small dark central stripe. Second segment in male yellowish grey with a triangular brown to black longitudinal stripe absent at the lower edge; in female with a narrow longitudinal band. Third segment in male with a dark longitudinal median band extending almost the whole length of the segment; in the female there is an incomplete band. Fourth segment in male with a faint dark longitudinal median band extending the whole length of the segment; in the female there are no markings on the fourth segment.

This species is widely distributed in India. It has also been recorded from Ceylon, Socotra, Cyprus, Senegal, Egypt and the Congo Free State. In South India it is the commonest blood-sucking muscid of cattle, and is found throughout the year.

Philaematomyia lineata is only found on cattle and about cow dung, especially where the latter is collected in heaps. On cattle it behaves in the same way as *Musca pattoni* and its allies, flitting about from place to place and sucking up the blood or serum which exudes from the bites of other flies. Although it is not a true biting fly it is clear, from the structure of its proboscis, that it belongs to the genus *Philaematomyia* (see page 48). Brunetti states that Dr. Annandale has seen this fly distended with blood while feeding on cattle, but this is no proof that it can obtain blood independently; it is quite common to find *Musca pattoni* and *Musca gibsoni* distended with fresh blood.

Bionomics and early stages of Philaematomyia lineata and insignis

Lineata lays its eggs, about thirty in number and of the muscid type, all together in cow dung; the larvae hatch in about ten hours and are mature in three days. The *larva* measures about 9 mm. in length and is of a lemon yellow colour. The *puparium* is of a dark mahogany tint.

Philaematomyia insignis may be seen burying its proboscis between the hairs on almost any part of the body of a cow, and the male sucks blood as voraciously as the female. Although blood is its main if not its only food both sexes have been seen applying their proboscides on the surface of fresh cow dung, in a manner which suggests that they suck up juice from the surface. Very occasionally the female has been seen to alight on human beings and dogs and to attempt to suck blood. When feeding the fly lies closely pressed against the skin of the host, its body being parallel with the surface. It remains in one position until replete with blood, and is not easily disturbed; it can, in fact, be easily picked off with the fingers. Like most blood-suckers, it passes out a clear watery fluid, and later unaltered blood, from the anus as the abdomen distends.

The female lays from forty to fifty or more eggs of a large size, all in one place, in isolated patches of freshly dropped cow dung rather than in larger collections of dried dung. On alighting, the female crawls over the surface until it finds a small crack or crevice; the ovipositor, which is similar to that of *Musca*, is now thrust into the dung, the abdomen being depressed, and all the eggs are deposited in a heap, from $\frac{1}{8}$ to $\frac{1}{4}$ of an inch below the surface. The process takes from six to ten minutes. When there are a large number of flies about, one often sees half a dozen or more all depositing their eggs in the same spot, their ovipositors being close to one another, while their heads are turned outwards. When the flies have finished laying their eggs an irregular heap of several hundreds will be found in the dung. On one occasion as many as thirty-six females were seen laying their eggs in one spot, their appearance suggesting a swarm of bees in miniature; five hundred and sixty eggs were collected later. When a group of females are laying their eggs all together in this manner, any new arrival will at once join them rather than select a place for itself. This gregarious habit is worthy of note and has not been observed in the case of any other muscid.

From the somewhat lethargic habit of the fly, especially when laying its eggs, and from the fact that it breeds rapidly and, in Madras at least, throughout the year, one would expect to find that it has many natural enemies, which keep down its numbers. The chief of these is a small Hymenopteron (not identified). The habit of this wasp is to settle on the dung and to watch for a fly laying its eggs. Having marked a victim, it crawls up to within an inch or two of it and then makes a short rapid flight, settles on the fly, and after stinging it carries it away, holding it by means of its sting and its hind legs; as many as five wasps have been seen on a patch of dung preying on *insignis*. The fly, busily engaged in laying its eggs, usually falls a ready victim, and this is specially the case when it has once inserted its ovipositor, as it often appears to have considerable difficulty in withdrawing it in time to escape from the wasp; when a number are ovipositing together the wasps carry them away in rapid succession. It also attacks the flies while feeding on cattle. Unfortunately the small size of the wasp and the rapidity with which it carries away its victim makes it difficult to locate its nest.

Several small species of spider also prey on *insignis*, catching them while laying their eggs. There is also a small Asilid which has the same habit, and can often be seen to swoop down on a fly and carry it off, grasped by its forelegs, to a neighbouring twig, where it sucks out its juices. Lastly, a small tachinid, which is commonly seen resting on a blade of grass close to a piece of dung in which *insignis* is laying its eggs, behaves in a remarkable and suggestive manner. It sits with its head directed towards the fly, and every now and then darts towards it, in a very direct and business-like manner, and at once returns to its perch. It certainly does not catch or attempt to catch *insignis*. It is a larviparous species, but as to how and where it deposits its larvae it is at present not possible to say.

The *egg* of *insignis* (Plate XLVI, fig. 3) is of the usual muscid type and measures from 2 to 2·2 mm. in length and ·4 mm. in breadth. The larvae hatch out in from eight to nine hours, that is, on the evening of the day on which the eggs were laid. When mature they measure 12 mm. in length, their greatest breadth being about one-seventh the length. They are of a bright lemon colour and on this account are readily distinguished from other muscid larvae. They all remain together feeding in the dung up to the evening of the second day, when they migrate in company, passing out from the lower surface; they bury themselves in the earth, and under leaves, etc., where they pupate. The puparium resembles that of *Musca*. It measures from 5 to 10 mm. in length and is of a light mahogany colour.

Both *Philaematomyia lineata* and *Ph. insignis* may be bred by employing the same technique as in the case of the non-biting, blood-sucking species of *Musca* (see page 355).

THE STOMOXYDINAE

Medium-sized flies of a greyish to brown colour, with four clove brown to black longitudinal thoracic stripes, and with bands and spots on the abdomen; front in male narrow; in female wide. Arista with seven to eleven bristles on its upper surface, and five on its lower; in some species, however, the lower bristles are wanting. Palpi shorter than, or as long as, the proboscis, often spatulate or club-shaped. Proboscis with the haustellum always greatly increased in length, so much so that when it is in the resting position it forms a conspicuous projection in front of the head. Labial gutter thickened, and the mentum consolidated to form a spindle-shaped tube, and only connected with the labial gutter by a narrow strip of membrane; the discal sclerite modified into two lateral plates connected ventrally on each side of the prestomum, and bearing at the distal ends the prestomal teeth. The pseudotracheal membrane is vestigial or entirely wanting. Thoracic chaetotaxy (macrochaetae):—Humeral 2 to 3; posthumeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post-alar 2; dorsocentral 3 to 5; acrostichal 1 or 2; mesopleural 10 to 12; sternopleural 1 or 2, sometimes 3, arranged 0 : 1, or 1 : 2. Wings clear or of a tawny olive colour, longitudinal veins with or without spines at their bases, but never with spines on the anterior border. First posterior cell open at its extremity; fourth longitudinal vein curved gently upwards. Reproduction oviparous, larvae cylindrical, with elongated and widely separated stigmata; puparium dark brown.

Bezzi gives the following Key to the Genera :—

1. Arista with bristles only on its upper surface 2
   Arista with bristles on both sides 4
2. Palps slender, much shorter than the proboscis; head in profile straight, height greater than breadth; eyes long and straight; posterior sinuosity well developed. Arista with ten to twelve straight bristles only on its upper border; one black sternopleural bristle arranged 0 : 1. Wings with first and third longitudinal veins spinulose at base, fourth curved upwards; first posterior cell broadly open . . . . . **Stomoxys**.

Palps as long or longer than the proboscis, sometimes club-shaped; head less straight; height equal to breadth; eyes round, and sinuosity less marked or even absent **3**

3. Proboscis short and solid, not pointed, labella distinct. Palps club-shaped, as long as proboscis, and curved upwards. Eleven to twelve bristles on upper surface of arista, long but not undulating; one black sternopleural bristle. Body robust; wing with first longitudinal vein nude, and third with spines at its base; fourth vein strongly curved, but straight after bend; first posterior cell narrowed . . . . . **Stygeromyia**

Proboscis long and pointed with rudimentary labella; palps straight, nearly linear, longer than proboscis, horizontal and appearing to adhere to it. Arista with six to ten bristles extending up to the summit, apical portion of arista much shorter than the bristles, which are undulating; two sternopleural bristles usually yellow, the posterior one small. Body slender; wings with all veins nude at base. First longitudinal vein terminating opposite the small transverse vein; fourth vein feebly curved and first posterior cell therefore widely open . . . . **Lyperosia.**

4. First and third longitudinal veins spinulose at base; female is distinguished from male by its colouration, particularly by its red legs. Body robust. Arista with five to eight bristles above, and three to four below. Palps as long as proboscis, and feebly club-shaped. Two sternopleural bristles of the same length. Fourth longitudinal vein curved after the bend; first posterior cell widely open . . . . . . **Haematobia.**

First and third longitudinal veins nude at base; no sexual dimorphism in the colour of the legs **5**

5. Body robust; palps strongly spatulate; arista with five to six bristles below; two sternopleural bristles. Fourth longitudinal vein feebly curved; first posterior cell broadly open . **Bdellolarynx.**

Body slender; palps feebly spatulate; arista with five to six bristles above and two below. Two black sternopleural bristles, the anterior small and sometimes absent. Fourth longitudinal vein strongly curved, then straight; first posterior cell straight at summit . . . . **Haematobosca.**

GENUS STOMOXYS, GEOFFREY

Medium-sized, greyish flies, some of them not unlike the house fly; their bodies are usually oval, and the head in profile is straight and of considerable height. The front in male at vertex is narrow, and in the female at centre about one-third total width of head. Arista with bristles only on its upper surface, usually eight to ten in number. Palps small, slightly cylindrical, and about half the length of the proboscis. Thorax somewhat longer than broad, usually with four clove brown to black longitudinal bands. Thoracic chaetotaxy *(macrochaetae);—Humeral 3; posthumeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post alar 2; dorsocentral 4 or 5, usually one small one in front of the suture; acrostichal 2; mesopleural 12; sternopleural 1, arranged 0 : 1. Abdomen usually marked with a dorsal stripe, bands and spots. Wings grey, sometimes tinged with yellow; fourth longitudinal vein with a looped curve, gently bending upwards to its extremity; first posterior cell broadly open.*

Identification of Species

The flies belonging to this genus are chiefly found in Asia and Africa, though *calcitrans* is now almost world wide in its distribution. Most of them are extremely difficult to identify, as no two specimens have exactly the same markings, and what is worse, the spots and bands vary according to the light in which they are examined; thus *calcitrans* has been described no less than seventeen times under different names. Miss Summers, who has recently studied the Oriental species, states that the characters most to be relied upon are: (1) The width of the frons in relation to the width of the head; (2) the width of the light median band on the thorax and (3) the colour of the legs. The abdominal markings are not reliable taxonomic characters, and should not be wholly used in distinguishing the species; *calcitrans* is a good example, as it shows great variation in this respect. Miss Summers recommends tracing the outline of the head and the median thoracic band with a camera lucida, using a low objective and eyepiece, and measuring the drawings. She gives the following key for the identification of the more important Oriental species:—

A.	Legs mainly black	1
B.	Legs mainly brown	2

A

1.	Frons in male wide, one-quarter, or one-fifth width of head	3
	Frons in male narrow, one-eighth or less width of head. Abdomen with round spots	**sitiens** (Male).
3.	Dorsal stripe on thorax narrow (·35 mm.) at anterior end, widening towards the posterior end. Abdomen spotted	4
	Dorsal stripe on thorax wide (·75 mm.), uniform in width. Abdomen banded	**nigra.**
4.	Spots round	**calcitrans.**
	Spots triangular, apex pointing to edge of segment	**triangularis.**
	Spots elongate	**oblongopunctata.**

B

2.	Frons wide, one-quarter to one-fifth width of head	5
	Frons narrow, one-sixth to one-eighth width of head	6
5.	Abdomen distinctly banded	7

Abdomen blotchy. Dark species. Fore tarsus in male with first joint fringed on the inside with a row of hairs of equal length . . . . **pulla** (Male).

7. Hind border of first three abdominal segments with a black band. Femora clove brown, hind tibiae ochraceous buff, frons, middle tibiae and tarsi mummy brown. Width of frons one-fifth in male, almost one-quarter in female. Frons in male constricted in middle . . . . **limbata.**

Dorsum of second abdominal segment entirely clove brown, deep posterior band on third segment. Frons and middle tarsi pale brown, width of front wider than one-quarter width of head . . . . **pusilla.**

6. Frons one-sixth in male, more than one-third in female. Femora dark brown, tibiae and tarsi pale yellow. Abdomen seen from behind at a very low level is banded . . . **pratti.**

Frons one-sixth in male. Interocular space very straight. Legs testaceous, coxae black, femora, brownish, anterior ones lighter on inner sides, darker on outer sides. Abdomen banded . . . . **indica.**

Stomoxys calcitrans, L. (Plate XLIX, fig. 1). Frons in male about one-fourth width of head, with fifteen fronto-orbital bristles; arista with eight or nine bristles on its dorsal surface; palpi small. In female the fronto-orbital bristles are irregularly arranged. Thorax, ground colour yellowish to whitish grey with four brown to black longitudinal bands, the outer pair interrupted at the suture. Abdomen, ground colour grey, sometimes yellowish, with a stripe on the second and third segments, not reaching the lower borders; two lateral circular dark spots on each segment. The fourth segment normally has a triangular basal spot or band which may be very indistinct or even absent. In addition this segment nearly always has two lateral stripes. The typical markings may, however, be very indistinct, and all small, while in some specimens the median stripes on the second and third segments fuse together and form one band, extending on to the fourth segment; the circular spots may be elongate and form transverse bands. In many specimens from Kodaikanal, South India, the abdomen was almost entirely black, and when this was noted it was found that the wings were more or less frayed and even broken in parts.

Relation to disease
Bionomics

In a recent paper on the transmission of polyiomyilitis through the agency of *Stomoxys calcitrans*, Rosebau and Brues describe some experiments in which they succeeded in infecting three monkeys out of twelve exposed to the bites of *Stomoxys calcitrans* which had previously bitten infected monkeys; this work has been confirmed by Anderson and Frost, who infected healthy monkeys with a culture obtained from those which had acquired the disease as the result of being bitten by this species. As this work is still in progress no comment is called for at present.

Stomoxys calcitrans has long been suspected of being the carrier of the trypanosome of Surra (*T. evansi*) and probably of other animal trypanosomes, but the evidence is so far inconclusive. Mitzmain has recently carried out a long series of experiments with this fly in order to settle this question. His results indicate that *Trypanosoma evansi* does not develop in *Stomoxys calcitrans*, and that it plays no part in the transmission of the parasite.

As is well known, this species chiefly bites cattle, horses, mules and donkeys, though it will occasionally bite man. If one stands near an animal on which a number of the flies are feeding one or more will bite about the ankles, even through thick socks. The other species the habits of which are known behave in the same way.

In Manila Mitzmain notes that *Stomoxys calcitrans* bites man shortly after the atmosphere has been cooled by a shower of rain, and at those seasons of the year when it is unusually abundant. He records the instance of a female coming into the laboratory after a shower of rain and alighting on his arm and sucking blood. Within an hour another settled close to the first one and also sucked blood; in this way altogether five flies attacked him, and it is interesting to note that three of them were males.

The flies are most abundant about stable and farm yards, and they may be seen basking in the sun on railings, the leaves of plants and blades of grass, especially where cattle are grazing. In Madras it is common during the cold weather; it never bites much before 9 a.m. The males may be seen hovering for short periods, darting at each other and then returning to the body of the animal or a neighbouring twig.

Life history of Stomoxys calcitrans

Portschinski appears to be the first observer to have made a detailed study of the life history of *Stomoxys calcitrans*; he confirmed the earlier observations of Bouché, who discovered the larvae in stable manure. Later Howard and Merlett repeated these observations, and bred the flies out of larvae collected in horse manure. In 1906 Newstead gave an account of the life history of *Stomoxys calcitrans* as observed in Liverpool and Chester. A most complete study of the early stages of this fly has recently been published by Mitzmain. The summary of the life history of *Stomoxys calcitrans* given here is taken from the papers of these two authors.

Stable refuse, especially when mixed with horse dung and urine, is a favourite breeding ground for *Stomoxys calcitrans*, but young larvae are rarely found in the upper layers if they have become dry. It is sometimes only necessary to turn over the superficial layers and expose the damp manure below when a number of females will be attracted to it and will commence to lay their eggs. In Chester Newstead noted that a heap of grass-mowings, the upper layers of which had only recently been deposited, contained a number of nearly mature larvae, whereas a neighbouring heap of horse manure which was dry did not contain any. At the King Institute, Madras, this fly regularly breeds in the sand in a Massachusetts sand-filter bed. The sewage effluent, as it trickles over the sand, forms a green scum, and here the females lay their eggs during December and January. In the Soudan Roubaud notes that the species frequent damp places, some more than others, and that the breeding grounds, as in the case of *Glossina*, are much more extensive during the rainy season than the dry weather, for they then usually migrate to streams and marshy ground. The females always deposit their eggs in the sand where there is much moisture and organic matter.

Newstead draws attention to the great difficulty often experienced in finding the natural breeding grounds of this fly; one of the writers had a similar experience recently at Kodaikanal, South India. The flies were swarming on cattle and horses, yet not a single larva was found in the locality, in spite of the presence of many suitable breeding grounds, such as large collections of horse manure; in one heap old pupal cases were found, but no larvae. A search was also made in the sand along the banks of streams where there was much organic matter, and where cattle came to drink. Although the flies were seen resting on the leaves of plants no larvae were found. There can be no doubt that *calcitrans* is somewhat particular as to where it lays its eggs, and that the one essential factor is the presence of an abundance of moisture.

Early stages of Stomoxys calcitrans

In the case of the filter bed mentioned above it has been noted that the flies deposited their eggs between 5 p.m. and 7 p.m., rarely during the day; this is, perhaps, explained by the fact that the filter bed is exposed to the sun during the greater part of the day. On alighting on the sand the fly crawls about for a short time, and then, rapidly depressing its abdomen, inserts its ovipositor into the sand and deposits three or four eggs, sometimes a dozen or more; Newstead notes that the eggs may be laid in a heap. According to Mitzmain oviposition takes place about nine days after the fly emerges from the pupa. From a number of observations made on flies bred and mated in the laboratory he gives the following data regarding the number of eggs laid by a single female:—

Length of time fly was kept Days	Number of depositions made	Total number of eggs
50	7	168
34	9	182
60	20	438
72	13	435
65	20	632
70	11	318
64	15	446

In addition to the eggs which were laid a number of ripe and unripe ones were found in the females after death. For instance, the fly which laid 632 eggs contained ninety ripe eggs and ninety-eight partially formed, so that this fly was capable of laying 820 eggs, which number Mitzmain considers to be the maximum a female is capable of producing.

The *egg* (Plate XLVI, fig. 4) is creamy white, elongate, curved on one border and almost straight on the other. The straight border has a deep furrow similar to that seen in the eggs of other muscids. The larva hatches in about twelve hours, and becomes mature in from seven to twenty-one days, the length of the period depending on the season of the year and the food supply.

The mature *larva* measures from 11 to 12 mm., and is of a dull white to creamy white colour; the posterior stigmata are black and almost circular. The anterior pair (Plate XLVI, fig. 6) are yellowish, and have five papillae. The feeding habits of the larvae are extremely characteristic; the anterior end is rapidly protracted and retracted, and the larva looks as if it were licking off the organic matter from the particles of sand; once this manoeuvre is seen, these larvae will be readily detected by it. When about to pupate they leave the moist sand or the dung and crawl to drier parts. The *puparium* is of a dark brown colour and measures about 5 to 5·5 mm. The pupal stage usually lasts about four days in the tropics, though according to Newstead it may be as long as thirteen in cool climates.

The alimentary tract of the larva of *Stomoxys calcitrans* is depicted in fig. 2, Plate L.

Breeding technique

It is relatively easy to induce most gravid females of *Stomoxys calcitrans* to lay their eggs if they are placed in cages either with horse manure, straw impregnated with urine and horse dung, or moist garden manure; the larvae may be successfully raised if the food is kept moist and free from moulds. This is accomplished by placing the cage in the sun for a considerable time, and adding to it small quantities of water; excessive moisture is to be avoided. In looking for the breeding places of any particular species of *Stomoxys* attention should be directed to horse dung, stable rubbish, manure heaps in gardens, the banks of streams and marshy ground; the larvae will be recognized by their characteristic habits when feeding. In Madras on two or three occasions a female has been seen depositing her eggs in a heap of cow dung; the larvae which hatched out did not, however, reach maturity.

Methods employed in keeping and feeding the flies

Mitzmain, in his recent paper on the rôle of *Stomoxys calcitrans* in the transmission of *Trypanosoma evansi*, describes the methods which he employed in feeding and keeping the flies alive for long periods in captivity. A screened stable was not satisfactory, owing to the large numbers of lizards and spiders which preyed on the flies; it was found impossible to prevent these from entering the stable. The writers found the same difficulty when experimenting with some species of *Tabanus*. Large bottles and museum jars were used by Mitzmain to confine and to feed large numbers of flies; the jar he figures is very similar to the one used by the writers (page 343). The longest time the flies were kept alive in these receptacles was thirty days; it was found advisable to transfer each fly to a single test tube after each feed towards the end of this period, about the twentieth day. As in the case of *Glossina* (see further on), it is difficult to prevent an excess of moisture collecting in the jars, even though a large quantity of filter paper is used. The large quantities of faeces passed by these flies and the condensation of moisture in the jar or bottle soon results in the early death of most of them; for this reason only a very few flies are placed in each jar. Mitzmain also found that cannibalism was common. If a fly was in any way disabled, especially after a recent meal, another active one attacked it, puncturing its abdomen. Mite infestation, which is common on most muscids, was also a serious hindrance when large numbers of flies were kept in the jars.

The best results are obtained by keeping each fly in a glass tube, and in this way Mitzmain kept *Stomoxys calcitrans* alive for ninety-four days. The tube used had a bore of 24 mm. and was plugged with cotton wool. A piece of white filter paper, of suitable size and kept moist, is placed in the tube; both paper and tube should be changed at least every two or three days.

Methods of applying the flies to the Host

In feeding a large number of flies, kept in a bottle, on a monkey, Mitzmain used the following method:—The monkey is strapped with its abdomen downwards to a table. The hair of the tail is closely cropped, and is then tied to a stout wire by means of gauze and passed through the neck of the bottle containing the flies. The other end of the wire is kept at a convenient distance from the mouth of the bottle in order to facilitate the manipulation of the tail. It is most important to immobilize the tail by fixing it to the wire, or the animal switches it against the sides of the bottle and crushes large numbers of the flies. Single flies may be fed on the monkey by inverting the tubes over the thighs; at least two flies can be fed at the same time in this way. It is not necessary to screen the mouth of the tube. When about to apply it, its base is directed toward the window light, the plug withdrawn and the filter paper pulled out with forceps; the tube is then inverted over the skin of the host. When the fly is replete a few taps on the glass will cause it to fly up; the tube is withdrawn, the filter paper replaced and the mouth of the tube plugged with cotton wool. The flies should be kept in the dark at a temperature of 20° to 26° C.

Flies can be fed on a guinea pig or other small animal by strapping it to a brass frame, which is passed into the jar containing the flies. The jar is held horizontally with the bottom towards the light. As soon as the flies have fed they collect at the bottom of the jar, being attracted by the light, and this is taken advantage of in order to remove and introduce them. When it is required to change the animal a few drops of chloroform or ether on the cloth cover facilitate its removal without killing the flies. It is best to shave the back of the animal.

Single flies in test tubes may be fed on small animals in the same way as on monkeys.

Large numbers of flies may be fed on the shaved abdomen of a calf or horse by strapping it down to a table; the skin of the animal should be moistened, as this attracts the flies. In the case of exact experiments with trypanosome-infected flies the skin should never be shaved, as

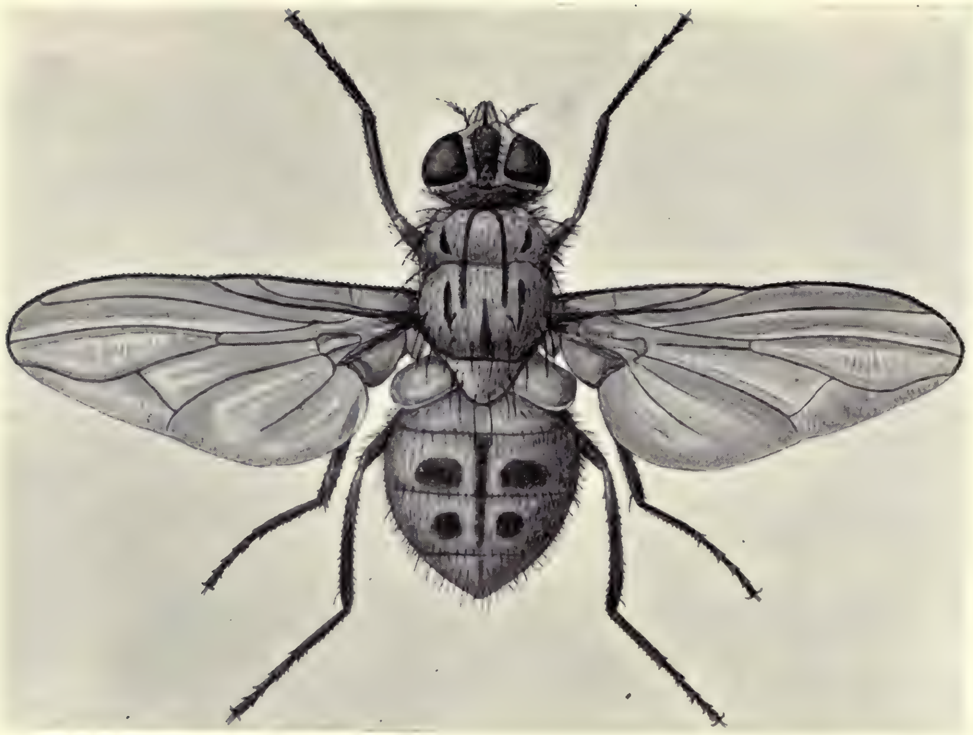

Fig. 1. Haematobia stimulans, ♀. × 10.

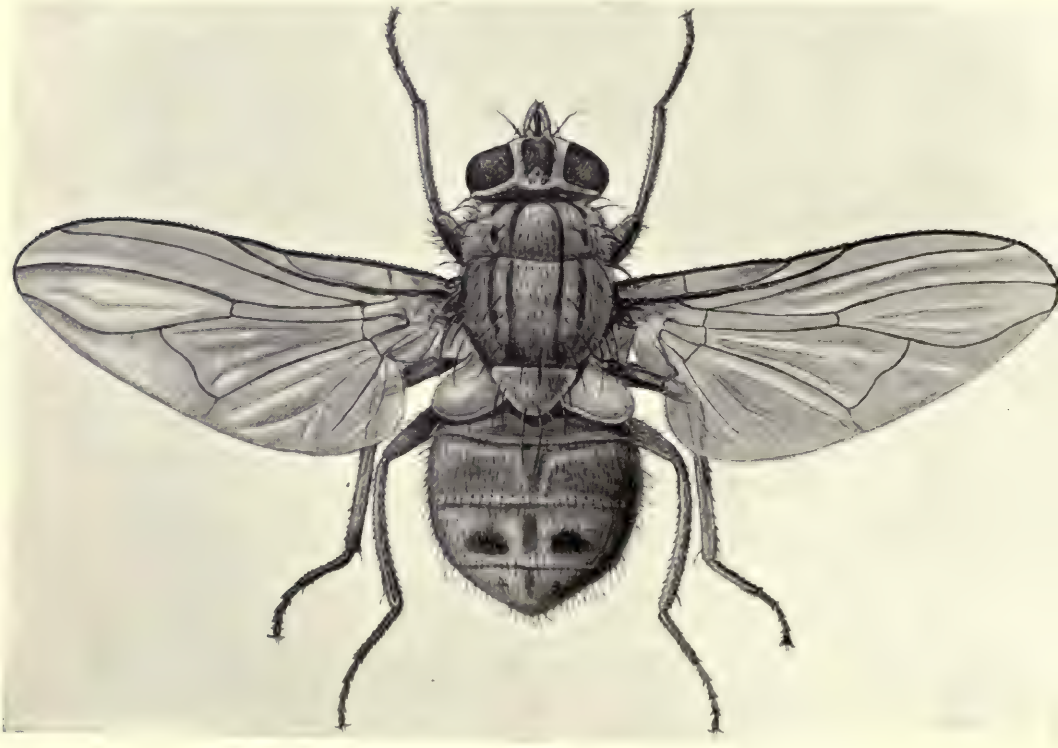

Fig. 2. Bdellolarynx sanguinolentus, ♀. × 12.

abrasions may result which will vitiate the experiments. In this case it is best to cut the hair close to the skin.

GENUS HAEMATOBIA, AUDINET SERVILLE

Medium-sized flies of a brownish yellow colour; body robust; head in profile not nearly as straight as in Stomoxys, and the posterior sinuosity of eyes much less marked. Sexual dimorphism marked, the males nearly always brownish throughout; the females are greyish with reddish yellow legs. Frons in male narrow, about one-eighth total width of head; in female about half total width of head. Arista with seven bristles on its upper surface, and two or three on its lower. Palp distinctly club-shaped, and as long as the proboscis. Thorax covered with fine bristles, and marked with four somewhat broad longitudinal bands. Thoracic chaetotaxy (macrochaetae):—Humeral 3; posthumeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post-alar 2; dorsocentral 4 or 5; acrostichal 1; mesopleural 10 or 11; sternopleural 2. Abdomen with a central longitudinal stripe, and lateral spots on most of the segments. Wings pale or tinged with yellow; first longitudinal vein spinulose or nude at its base; third vein always spinulose at its base. Fourth longitudinal vein curving upwards in its apical portion exactly as in Stomoxys; first posterior cell distinctly more broadly open than in Stomoxys.

Haematobia stimulans. Meigen. **Male.** Yellowish brown, with four somewhat broad longitudinal bands on the thorax, the outer pair interrupted at the suture. In many specimens there is an indistinct fifth band at the lower border of the mid-dorsum of the thorax. Abdomen with an interrupted somewhat narrow median longitudinal stripe, and a large triangular lateral spot on the second segment; a smaller circular spot on the third, and a still smaller spot on each side of the fourth.

Female. (Plate XLVIII, fig. 1.) Slate grey to yellowish grey, with very much narrower admedian thoracic bands than in the male, and with two lateral spots; abdominal markings as in the male, except that the lateral spots on the fourth segment are wanting. Legs reddish yellow.

This species is widely distributed in Europe from the north to the south. Its breeding habits and early stages are very similar to those of *Stomoxys*, and have been studied by Portschinski.

Haematobia sanguisugens, Austen. This species is allied to *stimulans* but differs in the following respects; it is distinctly smaller, and the central longitudinal stripe on the abdomen is continuous throughout its length ; the fourth segment of the male has no lateral spots, and the first longitudinal vein has only one or two spines at its base.

It is found in Northern India, at Kasauli in the Western Himalayas, and at Darjeeling in the Eastern Himalayas. It feeds on cattle and horses; its early stages are unknown.

GENUS BDELLOLARYNX, AUSTEN

Medium-sized flies of a mouse grey, greenish or brownish grey colour, very closely allied to Haematobia, with which the only species may be confused. Body robust, and head in profile similar to that of Haematobia. No sexual dimorphism, except perhaps in the male. Frons in male one-eighth to one-ninth total width of head; in female one-half total width of head. Arista with eleven long bristles on its upper surface, and five on its lower. Palp club-shaped, and as long as the proboscis. Thorax covered with small bristles as in Haematobia, and with four very narrow longitudinal stripes. Thoracic chaetotaxy (macrochaetae):—Humeral 2; posthumeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post-alar 2; dorsocentral 5, two of which are in front of the suture and three behind; acrostichal 1 or 2; mesopleural 10 to 12; sternopleural 2, arranged 0 : 2. Abdomen yellowish brown, with a median longitudinal brown band, and lateral brown patches; wings grey, tawny in male. Fourth longitudinal vein curving upwards less abruptly than in Haematobia, and the first posterior cell broadly open; first and third longitudinal veins without bristles at their bases.

The only species, *Bdellolarynx sanguinolentus*, Austen, (Plate XLVIII, fig. 2) though very closely allied to *Haematobia*, may be distinguished as follows:—By the absence of sexual colour dimorphism, and by the longitudinal bands on the thorax being narrower; by the broader frons of the male; by the number of bristles on the arista, and by the absence of spines on the bases of the first and third longitudinal veins. *Bdellolarynx sanguinolentus* is found in many parts of India, and has been recorded from Bombay, Calcutta, and Mussoorie; Allahabad, Nepal, Sylhet, Lower Burma, Travancore and Ceylon. One of the writers collected some hundreds of specimens at Kodaikanal (6,000 ft.) Pulney Hills, South India.

Both sexes are voracious blood-suckers, and feed on cattle and horses. Like *Philaematomyia insignis*, they can be readily caught in the fingers. The male has the habit of hovering under the belly of the host, or near small twigs and branches, remaining in the air for a few minutes and then returning to its resting place, to repeat the manoeuvre after a short time.

Although a most vigorous search was made for the larvae in Kodaikanal, they were not found. A few were bred in cow dung, but with great difficulty. The *egg* is almost black when laid and in general structure simulates that of ***Stomoxys.***

GENUS HAEMATOBOSCA, BEZZI

Medium-sized brownish flies very similar in general appearance to Haematobia and Bdellolarynx, but with slenderer bodies. The head in profile is not unlike that of Haematobia. There is no sexual colour dimorphism. Frons in male narrow; in female about half the total width of the head. Arista with six to seven bristles on its upper surface, and one to two on its lower. Palp as long as proboscis, but less club-shaped than in Haematobia and Bdellolarynx. Thorax covered with small bristles and marked on its dorsum with four narrow longitudinal bands. Chaetotaxy as in Bdellolarynx. Abdomen with a central longitudinal band and lateral brown patches. Wings greyish or tawny; fourth longitudinal vein curves up to a greater extent than in the case of Haematobia and Bdellolarynx. The first posterior cell is narrowly open as in Stygeromyia (at least S. maculosa). First and third longitudinal veins without any basal spines.

Haematobosca atripalpis, Bezzi, the type species, is found in Central Europe. The only other species, *H. perturbans*, Bezzi, is found in North China. The early stages of both these flies are unknown.

GENUS STYGEROMYIA, AUSTEN

Medium-sized flies resembling Stomoxys and Lyperosia in general appearance. Head flattened somewhat from before backwards. Frons at vertex in male narrow, about one-third total width of head. Arista with eleven or twelve bristles on its upper surface, none on the lower. Palpi as long as the proboscis, club-shaped and curving upwards. Thorax greyish, with two or more clove brown stripes. Thoracic chaetotaxy (*macrochaetae*) *:—Humeral 3; posthumeral 1; notopleural 2; presutural 1; supra-alar 1; intra-alar 1; post-alar 2; dorsocentral 6, one in front and five behind the suture; acrostichal 1; mesopleural 9 or 10; sternopleural 1, arranged 0 : 1. Abdomen greyish with spots and longitudinal median band. Wings pale to clove brown; first posterior cell narrowly open at the tip; apical portion of fourth longitudinal vein perfectly straight and not bent up at the extremity, or only slightly so.*

Stygeromyia maculosa, Austen. **Male.** Thorax, ground colour grey, with a pair of narrow admedian stripes extending to the posterior border, and two broader spots on each side near the transverse suture, one in front of suture immediately behind the posthumeral bristle, and the other behind the suture; these thoracic markings are similar to those of the female *Haematobia stimulans* (see Plate XLVIII, fig. 1). Abdomen rounded, first segment without markings; second, third and fourth with elongated median brown spots, as well as spots at the sides, those on the second segment being the largest. Female unknown. This fly is found in Aden; its breeding habits are unknown.

Two other species, *S. sanguinaria*, Austen, and *S. woosnami*, Austen, have been recently described from Africa; the latter was caught in the act of biting.

GENUS LYPEROSIA, RONDANI.

Very small to small flies, slate grey or greyish yellow to dark grey in colour, with elongated bodies; the abdomen usually twice as long as broad. Frons in male very narrow, one-seventh to one-eighth total width of head; in female one-third total width of head. Arista with somewhat long undulating bristles, on its upper surface only. Palp stout and almost uniformly broad throughout its length; it is as long as the proboscis, to which it is closely applied. Thorax slate grey to dark grey, with four well defined or indistinct dorsal stripes; sometimes spots in addition. Thoracic chaetotaxy (macrochaetae):—Humeral 2; posthumeral 1; presutural 1; notopleural 2; supra-alar 1; intra-alar 1; postalar 1; dorsocentral 10, sometimes 12, mostly small; acrostichal 1 behind suture and a row of four smaller bristles in front; mesopleural 6 to 8; sternopleural 3, arranged 1 : 2. Abdomen slate grey to dark grey with a central longitudinal stripe on one or more segments. Wings hyaline, fourth longitudinal vein curved gently upwards but much straighter than in Stomoxys, Haematobia or Bdellolarynx. First longitudinal vein joining the margin opposite to, or in front of the inner cross-vein. Third longitudinal vein without spines at its base; first posterior cell broadly open.

The flies of this genus are of some importance, as they appear to be the nearest allies of those of the genus *Glossina*. The structure and position of the palps in relation to the proboscis, and also the scissor-like position the wings assume when at rest, strongly recall *Glossina*. *Lyperosia exigua*, Meij., however, often holds its wings upwards when resting. They can be distinguished from most other species of the

Stomoxydinae, especially those of *Stomoxys* and *Stygeromyia*, by noting that the nude apical part of the arista is shorter than the last bristle, whereas in *Stomoxys* the nude apical part is longer, or as long as the last bristle; the eyes are rounder and the wings straighter. The posterior stigmata of the larva and pupa, as far as is known, are closer together than is the case in the other Stomoxydinae; the stigmal slits are narrow and convoluted as in the larvae of the genus *Musca*.

Lyperosia is essentially an Old World genus, and the species have probably been introduced into the New World by man. Bezzi has published a valuable paper on the genus; he gives the following key to the identification of the better known species.

Bezzi's Key to the Species of Lyperosia.

1.	Sixth longitudinal vein very long, always longer than the distance between its extremity and the posterior margin; first longitudinal vein ending at the margin opposite the inner cross-vein. First posterior cell narrow at its extremity. Eight to ten aristal bristles close together. Hind tarsi in the male serrated and dilated; hind tibiae with a long pre-apical bristle. Large-sized species (3·5 to 5 mm.)	**2**
	Sixth longitudinal vein short, shorter than its distance from the posterior margin; first longitudinal vein joining the margin just before the small transverse vein. First posterior cell not so narrow at its extremity. Six aristal bristles, generally separated. Hind tarsi of male simple; pre-apical bristle of hind tibiae short. Small acrostichal bristles regularly arranged in four longitudinal rows. Species of small size (2 to 3·5 mm.)	**6**
2.	Anterior acrostichal bristles longer, and irregularly arranged in a row of six; aristal bristles close together; halteres yellowish. Antennae, palps and legs nearly always dark brown to black. Species larger; Europe, Africa and America . .	**irritans.**
	Anterior acrostichal bristles short and regularly arranged in longitudinal rows; aristal bristles not so close together; halteres white. Antennae, palps, and legs often clear yellow; sixth vein a little shorter. Small species (3·5 to 4 mm.) Central Asia and the neighbouring parts . .	**exigua.**
3.	Body dark, markings on abdomen distinct. All macrochaetae and bristles black except those of peristomum and propleural tuft, which are yellow. Frontal band black with white pubescence; proboscis glossy black, sometimes reddish. Antennae palps and legs black, cheeks and anterior tibiae pale, sometimes basal segments of antennae are reddish. Wings light with black veins. Length 3·5 to 4·5 mm. North and Central Europe and North America . . .	**irritans** variety **typica.**

Body not so dark, greyish ; macrochaetae and bristles of mesopleura either entirely yellow or only partly so ; palps pale yellow. Proboscis and basal segment of antenna red or yellow ; legs pale, wings hyaline ; veins yellow **4**

4. Bristles and macrochaetae of scutellum entirely black or only partly so ; bristles of abdomen black ; markings on abdomen somewhat dark ; femora always black. Palps and basal segments of antennae dark yellow. Large sized species **5**

Bristles and macrochaetae of thorax and abdomen clear yellow. Longitudinal band of abdomen distinct or absent ; femora sometimes yellow ; palps and basal articles of antennae clear yellow. Small sized species (3·5 to 4 mm.) North Africa . . . . **irritans** variety **weisii.**

5. Frontal band red or reddish ; length 4 to 4·5 mm. North America and Hawaian Islands . . . . **irritans** variety **rufifrons.**

Frontal band black with greyish pubescence ; length 4 to 5 mm. Central Europe . . . . **irritans** variety **meridonialis.**

6. First posterior cell narrow at the summit ; frons of male rather broad, the central stripe as broad as the eye ; legs almost entirely pale. Length 1·8 to 2·8 mm. Ethiopian species . **minuta.**

First posterior cell open ; frons of male straighter, central band as broad as the eye ; legs blackish. Length 2·5 to 3·5 mm. From Central Europe . . . . **titillans.**

Lyperosia irritans, L. A large dark grey to yellowish grey species. Frons of male about one-seventh total width of head ; frons of female about one-half total width of head. Thorax with four somewhat ill-defined dark bands, the outer pair not reaching the anterior margin. Abdomen with a dorsal longitudinal median stripe on second segment, elsewhere dark grey. Palpi flat and spatulate at tips. First posterior cell narrowly open.

This species is found throughout Europe and in America, where it is said to have been introduced about the year 1886 ; it soon spread all over the United States and the greater part of Canada. It was first noticed as a serious pest in the vicinity of Philadelphia ; probably the fly was first landed at this port.

Lyperosia minuta, Bezzi. A very small dark grey to brownish yellow species. Frons in male extremely narrow ; in female one-quarter total width of head. Thorax dark, grey to yellowish brown, with two dark brown lateral stripes, one on either side of a broad grey central band. Abdomen dark grey to olivaceous grey, without any distinct markings. First longitudinal vein ending opposite the small cross-vein ; first posterior

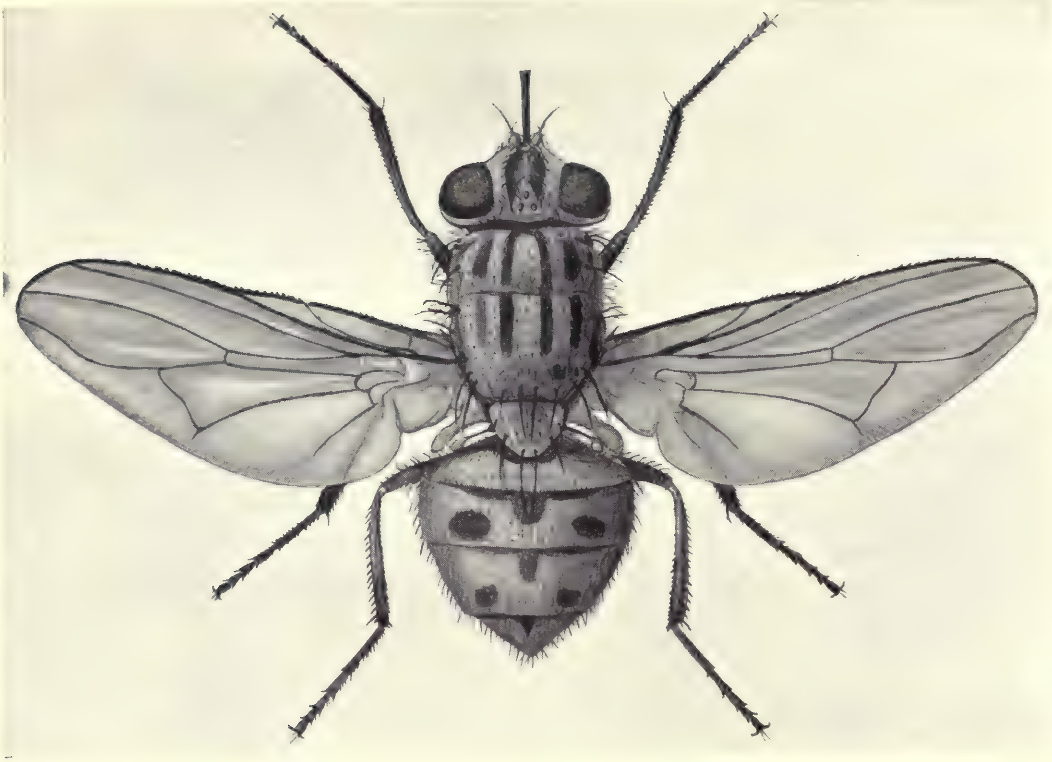

Fig. 1. Stomoxys calcitrans, ♀. × 10.

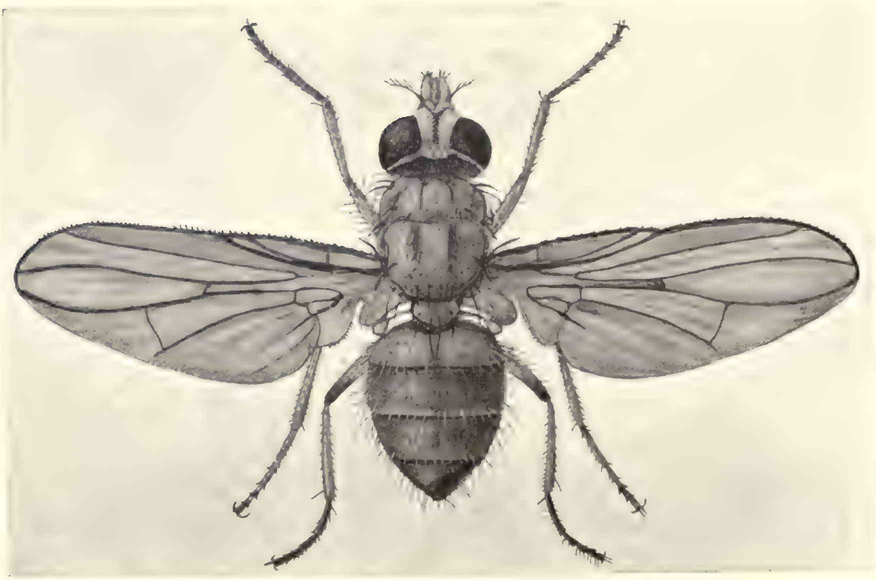

Fig. 2. Lyperosia exigua, ♀. × 16.

cell widely open. Palpi dark and slightly spatulate at their tips. This species is found almost throughout India and Ceylon, and Africa; it was originally described from Somaliland.

Lyperosia exigua, Meij. (Plate XLIX, fig. 2.) A larges late grey to dark grey species. Frons in male about one-fifth total width of head; in female one-third. Thorax, ash grey to dark grey, with two narrow well-separated brown stripes. Abdomen dark grey, lighter at the upper end, with a distinct narrow dark longitudinal median band on the first and second segments. Palpi narrow and spatulate at tips. Third and fourth veins converging towards their extremities, and first posterior cell narrowly open. It is found throughout India, in Java, and other parts of Central Asia.

Bionomics

Lyperosia irritans, the type species of the genus, is popularly known in the United States as the 'Horn fly' from its habit of resting on the horns of cattle; *minuta* and *exigua* also have this habit. Farmers and stockbreeders in the United States believe that *irritans* deposits its eggs on the horn, and that when the larvae hatch out they burrow into the skin and even penetrate the brain. It is probable that this idea receives support from the fact that when a large number of flies collect on the horn, the black excreta give it a speckled or 'fly-specked' appearance.

When at rest the flies nearly always fold their wings in a scissor-like manner over the abdomen; when feeding they elevate their wings. *Exigua* may often be seen on cattle, resting between the shoulders, or higher up between the horns. All the species feed on the back and flanks, seldom on the legs and abdomen.

Breeding habits and early stages

All the species of the genus *Lyperosia* lay their eggs in freshly dropped cow dung. The females settle on the dung the moment it falls to the ground, and lay the eggs either on the surface of the dung or in cracks; only one egg is laid in each place and at each act. *Exigua*, whose habits have been observed in Madras, usually lays about twelve eggs at a time. The flies immediately return to the cow and the process is repeated when dung is again dropped. The egg measures about 1·2 mm. in length, and is of a light reddish colour, straight on one side and convex along the other; it has a deep furrow on the upper surface of the straight border and the ends are spatuloid. The mature larva measures about 7·5 mm. in length, and is of a dirty white colour; the posterior stigmata are close together; otherwise it is very similar to the larvae of the other Stomoxydinae. The larvae migrate from the dung when about to pupate, and the puparia are always found in the earth at some distance away, or under the sides of the patch of dung. The puparium measures about 4·5 mm. in length and is dark brown in colour ; the fly usually hatches out in five days, though sometimes as late as the eighth day.

Weiss has studied the life history of *irritans,* variety *weissii,* from Algeria ; its larval stage lasts five days, and the flies hatch out of the puparia in another five days. Recently hatched flies will readily feed on the human arm.

Owing to the peculiar circumstances under which these flies lay their eggs it is necessary, in order to breed them, to watch freshly dropped cow dung in the field. If there are large number of flies on the cow one or more of the females will almost certainly alight on the dung and lay a number of eggs. The dung should be transferred at once to a tray with some sand in it, and taken to the laboratory. If it is regularly placed in the sun, the larvae will be found in it in a few days ; they can be recognised by noting the character of the posterior stigmata.

Breeding Technique

The female flies will readily lay their eggs in test tubes, especially if some fresh cow dung is placed at the bottom ; Weiss notes the same with the Algerian species. In the case of *exigua* and *minuta,* for some unknown reason, as often as not the eggs do not hatch out. Weiss does not appear to have had any difficulty in rearing larvae from eggs laid in dung in a test tube.

The methods described in keeping and feeding *Stomoxys* should apply equally well to *Lyperosia.*

THE GLOSSININAE

Genus Glossina, Wiedemann

Narrow bodied, elongate flies of a yellowish to dark brown or black colour, varying in size from 6 to 13·5 mm. Width of frons in male from one-third to one-half total width of head ; in female about one-half. First two joints of antenna small, but the third joint long, and of a characteristic shape, concave anteriorly, and ending in a forwardly directed point. Arista three jointed, the first two joints small and inconspicuous, the third broadly elongated and slightly tapering at its extremity, and adorned on its upper surface with from seventeen to twenty-nine delicate curved, branching bristles. Proboscis long, projecting horizontally forwards, and covered by the long hollowed out palps, which are not swollen or pointed, but of uniform width throughout their length.

PLATE L

Figure 1. The alimentary tract of the larva of *Tabanus albimedius.* oes., oesophagus. pv., proventriculus. sl.g., salivary gland. mg., mid-gut. mp.t., Malpighian tubes. × 3½.

Figure 2. The alimentary tract of the larva of *Stomoxys calcitrans*, dissected out. sl.d., salivary duct. ph., pharynx. ch.t., chylific tubules. h.g., hind-gut. v., valve-like constriction on the hind-gut. Other letters as above. × 10.

Figure 3. The chitinous framework of the pharynx and connected parts of the larva of *Stomoxys calcitrans.* lr., labrum. × 66.

Figure 4. The head of the larva of *Tabanus albimedius*, showing the mouth appendages. lr., labrum. p., palp. mx., maxilla. ant., antenna. md., mandible. sp., the area of spines. Drawn from a cleared preparation. × 66.

PLATE.L.

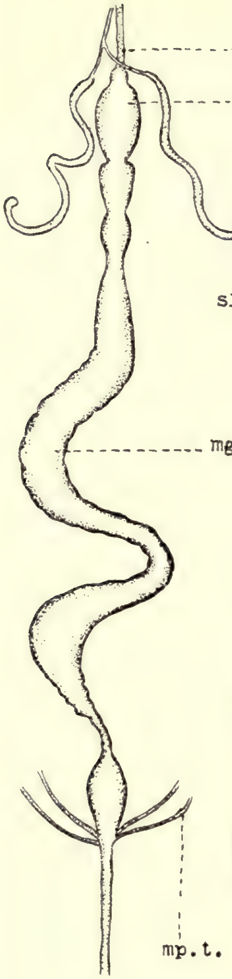
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Fig. 1.

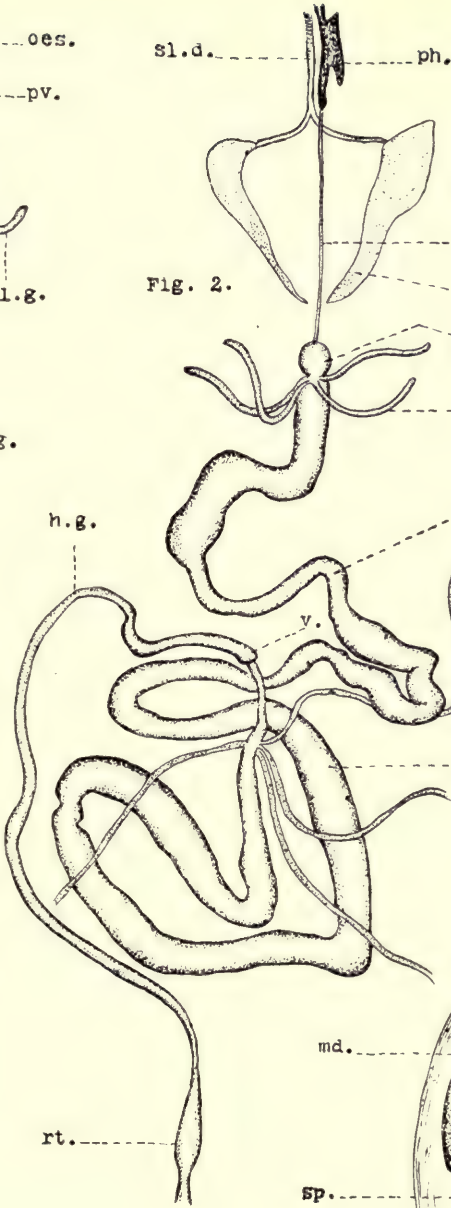
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Fig. 2.

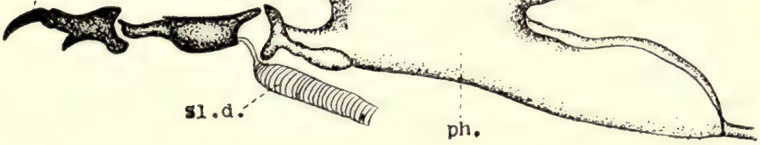

Fig. 3.

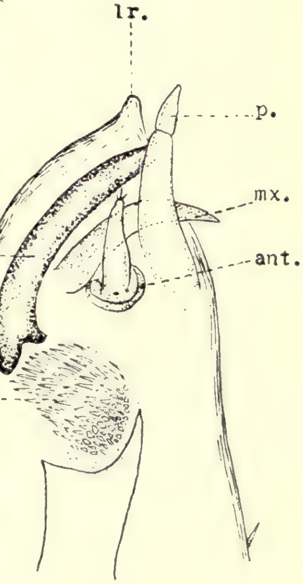
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Fig. 4.

Thorax marked with inconspicuous greyish brown stripes or spots. Chaetotaxy (*macrochaetae*) *:—Humeral from 1 to 3, sometimes 4, the lowest bristle the largest ; posthumeral wanting ; notopleural 2 ; presutural 1 ; supra-alar 1 ; intra-alar 1 ; post-alar 3 ; dorsocentral 3, one anterior to the suture and two posterior ; acrostichal 1 ; scutellar 2 ; prothoracic 1 ; stigmatic 1 ; mesopleural 6 ; pteropleural 3, besides several smaller ones ; sternopleural 3, arranged 1 : 2. Abdomen yellowish to dark brown, consisting of eight segments, seven only visible, the first being concealed beneath the scutellum. Male hypopygium characteristic in shape* (see page 87). *Wing venation characteristic, veins concentrated along the anterior half of wing ; membrane rilled. The fourth longitudinal vein is bent downwards in its basal portion, but about the middle of the wing bends sharply upwards ; in its apical portion it passes obliquely downwards, again bending up to reach the margin of the wing some distance anterior to the apex ; the second, third and fourth longitudinal veins all turn upwards at their extremities. The anterior transverse vein is very oblique. Reproduction larviparous, larva born when ready to pupate. Puparium with characteristic protuberances.*

The Glossininae or 'Tsetse flies,' as they are popularly called, are next in importance to the Culicinae among the blood-sucking Diptera. Through the researches of Koch, Bruce and his collaborators, Kleine and his co-workers, and a host of others whose names are not so familiar, it is known not only that *Glossina palpalis* and *G. morsitans* convey to man by their bites *Trypanosoma gambiense* and *T. rhodesiense*, but exactly how and under what conditions these flies can infect man. This knowledge has been of fundamental importance in the fight against Sleeping Sickness in Tropical Africa. In addition, several trypanosomes which cause fatal forms of animal trypanosomiasis are known to be transmitted by one or more species of *Glossina*.

A fresh impetus has been given to the study of these flies owing to the fear of the spread of human trypanosomiasis into South Africa, and workers of all nationalities are now engaged in working out their life histories and geographical distribution, and their relations to human and animal trypanosomiasis. Fortunately for man and his domesticated animals, the tsetse flies, with one exception, (*G. tachinoides*, West.) are only found in Africa.

Owing to the importance of these flies it is necessary to give a somewhat detailed account of every species. In compiling what follows Austen's valuable and indispensable *Handbook of the Tsetse Flies* has been freely used: also Newstead's important papers on the structure of the male genitalia, and Roubaud's thesis on *Glossina palpalis*, one of the most important works on the subject. Other papers in the *Bulletin of Entomological Research* have also been consulted, as well as the summaries of recent work in the *Sleeping Sickness Bulletin* and in the *Tropical Diseases Bulletin.*

Classification of the Glossininae

In classifying these muscids Newstead's scheme, which is based on the structure of the male external genitalia, will be followed. This observer rightly says that the structure of the external genitalia must be the best guide to the affinities existing between the several species. A description of the external genitalia of *Glossina* is given on pages 87 and 88.

NEWSTEAD'S KEY TO THE SPECIES OF GLOSSINA

Newstead divides the genus *Glossina* into three groups as follows:—

Group 1. THE FUSCA GROUP. In this group are placed the seven largest species of the genus; *G. fusca*, Walk., *G. nigrofusca*, Newst., *G. tabaniformis*, Westw., *G. longipennis*, Corti, *G. brevipalpis*, Newst., *G. medicorum*, Aust., and *G. severini*, Newst. In these species the superior claspers are entirely free, and have no membrane between them; their distal extremities have either a single large blunt tooth-like extension, or they are bluntly bidentate; the harpes present differences in structure in all the species.

Group 2. THE PALPALIS GROUP. The following species are placed in this group:—*G. palpalis*, R.-D., *G. calignea*, Aust., *G. tachinoides*, Westw., *G. fuscipes*, Newst., and *G. pallicera*, Bigot. In these species the superior claspers are connected by a delicate spinose membrane which is deeply divided in the middle, but the distal extremities of the claspers are free and widely separated.

Group 3. THE MORSITANS GROUP. This group contains the following species:—*G. morsitans*, Westw., *G. submorsitans*, Newst., *G. pallidipes*, Aust., and *G. longipennis*, Wied. In these species the superior claspers are completely united by a spinose membrane, and are also fused in the middle line; they are highly complicated, and Newstead compares their shape to that of the scapula of a mammal in miniature.

Utilizing the above differences in the structure of the external genitalia, Newstead gives the following key for the identification of the species.

Group 1 (*Fusca* Group). Large species, length exclusive of proboscis **10¾ to 12 mm.**

A. Thorax with the usual longitudinal markings more or less distinct.

Palpi relatively long and thin. Thorax russet brown, markings distinct, areas enclosed by the curved lines becoming gradually paler outwardly. Third segment of the antenna clothed with very short pubescence. Harpes of male with a strongly serrated margin ; median process not extending beyond the inferior claspers. . . . . . **fusca.**

Palps as in *fusca*. Thorax smoky brown, pale markings sharply and clearly defined. Third or terminal segment of antenna clothed with very long pubescence, and with apex strongly recurved. Harpes of male not serrated, median process projecting moderately beyond the inferior claspers. **nigrofusca.**

Palpi relatively short and stout. Thoracic markings not very clearly defined. Third segment of antenna with very short pubescence. Median process in the armature of the male more than twice the length of the inferior claspers ; harpes not serrated . . . . **brevipalpis.**

B. Thoracic markings reduced to spots.

Thorax with four (sometimes six) dark brown oval spots, the four larger ones arranged in a parallelogram. Harpes of male clothed with large squamose spines . . . . . **longipennis.**

C. Without such spots.

Lateral branches of hairs of arista very long, the terminal one about half the length of the free end (tip) of the shaft. Harpes of male with four narrow pointed appendages. . **tabaniformis.***

Lateral branches of the hairs of the arista very short, the terminal one about one-fifth the length of the free end of the shaft. Harpes of male with one broadly lanceolate appendage. . . . . **medicorum.***

Lateral branches of the hairs of the arista relatively long. Harpes of male rudimentary with distal margin irregularly serrated . . . . **severini.***

Group 2 (*Palpalis* Group). Hind tarsi all dark. Length 7 to 9½ mm.

Thorax, legs, and abdomen spotted. . . . . . . **maculata.**

Abdomen very dark brown or blackish brown, with a small median pale triangular area on second segment, extending distally as a very narrow stripe. Inferior claspers of male with a long broad stem to the foot-like terminal process ; superior claspers straight, rapidly narrowing distally and terminating in a conical point . . . . **palpalis.**

Similar to *G. palpalis*, 'but browner and somewhat larger ' . . . pale area on second segment broad and more ' or less quadrate or irregular in outline . . . dorsum, ' of seventh abdominal segment . . . often cream buff'. (Austen). Superior claspers of male with a terminal tooth-like extension one-third the length of the clasper. . . **calignea.**

Small and slenderly built. Abdomen pale, with distinct transverse blackish bands ; median pale stripe very distinct. Legs, with the exception of the hind tarsi and the tips of the front and middle ones, pale yellowish. Inferior claspers of male with a very short stem to the foot-like terminal process; superior claspers as in *palpalis*. . . . **tachinoides.**

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* Not included in original Key.

Small and stoutly built. Abdomen as in *palpalis*, but with the usual transverse dark bands more evident. Thorax dusky grey with four greyish-black, triangular blotches. Legs almost uniformly infuscated. Superior claspers of male curved and terminating in a claw-like point. . . **fuscipes.**

Abdomen almost unicolorous, but darkening gradually towards the margins posteriorly. Superior claspers of male straight and gradually narrowed, truncate and spinose at the apex . . . . **pallicera.**

Group 3 (*Morsitans* Group).

A. Tips of hind tarsi only dark or black.

Both sexes with the front and middle tarsi yellow. Third segment of antennae long and narrow, apex pointed. Superior claspers in male very similar to those of *longipalpis*, with a flange-like projection internally, the breadth of which is greater than the width of the stem of the clasper at the point of its origin. . . . . . . **pallidipes.**

B. Tips of all the tarsi dark or black.

Abdomen often with a large dusky red-brown area transverse bands on third segment may be either widely separated and faintly indicated medially, or strongly pronounced and narrowly separated. Superior claspers in male terminating in a tooth-like process on outer angles, the internal flange-like projection much narrower than stem of clasper, and not produced distally into a median lobe. **longipalpis.**

Abdomen with the median stripe usually much wider on the third segment than on the fifth. Median lobes of the superior claspers in male converging distally; outer angle of claspers without any tooth-like process . . . . . **morsitans.**

Abdomen with the transverse bands sharply defined medially, median stripe usually of uniform width on the third, fourth and fifth segment. Median lobes of the superior claspers parallel; outer angle of claspers without any tooth-like process . . . . **submorsitans.**

Glossina palpalis, Robineau-Desvoidy. (Plate LI, fig. 1.) A dark medium-sized species; length of male, according to Austen, 8 to 9 mm.: length of female 8·6 to 10·2 mm. Thorax bluish grey to olive grey, with brown markings which are described by Austen as follows:—'A narrow 'stripe on each side of the median line, interrupted before reaching the 'transverse suture, and again before reaching the hind margin; the section 'of each stripe behind the suture is expanded posteriorly, and the terminal 'portion of the stripe immediately in front of the hind margin takes 'the shape of a pair of more or less confluent ill-defined spots, sometimes

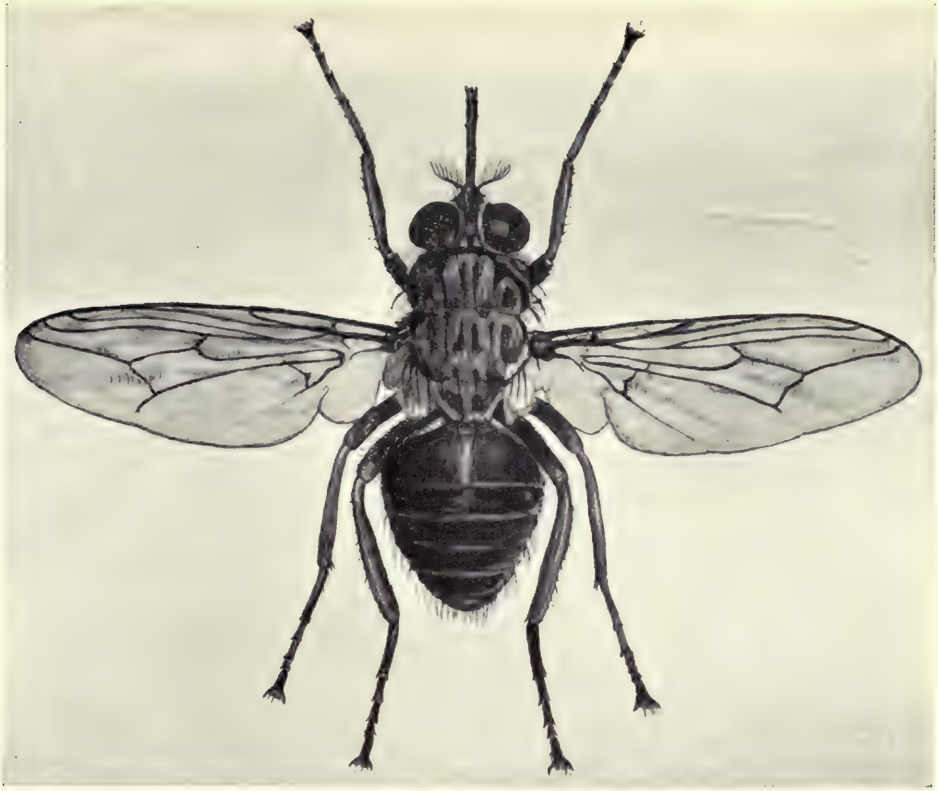

Fig. 1. Glossina palpalis, ♂. × 6

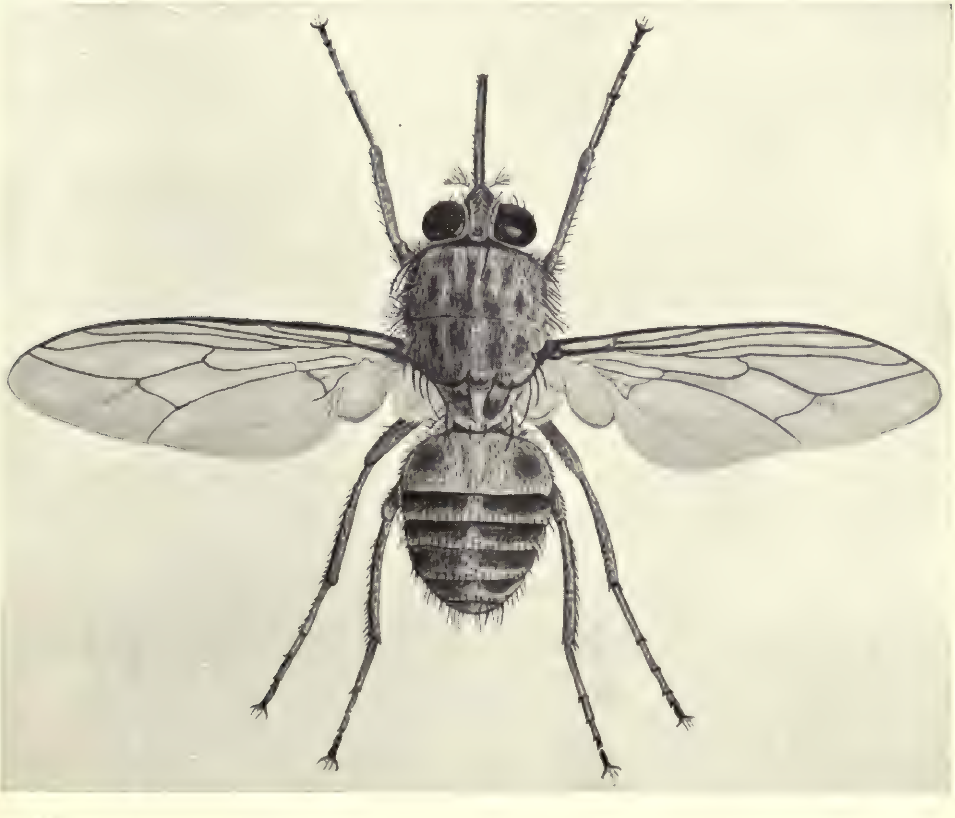

Fig. 2. Glossina morsitans, ♀. × 6

'confluent with the stripes in front; next to the two admedian stripes on 'each side, on the suture itself, a more or less sharply defined oval spot; 'on the outside of this a longitudinal stripe, more or less interrupted and 'sometimes obsolete in the middle, but in the front, curving round outwards behind the humeral callus and then running backwards along the 'lateral margin of the dorsum nearly to the post-alar callus; in the area 'thus enclosed a broad ill-defined patch in front of, and behind, the 'suture, while the lateral stripe itself sends off two prolongations, which 'run inwards for a certain distance on each side of the suture. Humeral 'callus with a spot on its upper portion, confluent with the curved stripe 'behind it; a more or less ill-defined spot on the post-alar callus also.'

Abdomen dark brown; first segment with a pale triangular area, its base directed towards the anterior, and its apex towards the posterior margin of the segment; second segment with a much smaller pale triangular patch than on the first segment, its apex being continued either as a faint or more distinct stripe down the centre of the abdomen as far as the posterior margin of the fifth segment; edges of all the segments grey, the entire seventh grey, as well as the hypopygium.

Glossina palpalis may be confused with *G. fuscipes*, Newstead and *G. calignea*, Austen. According to Newstead it is distinguished from the former by its larger size, and by the thorax not being dusky grey, or the legs uniformly dusky. According to Austen it is distinguished from *G. calignea* by its head being distinctly narrower, the arista shorter and stouter, the abdomen blacker, the median pale area on the second segment being cuneate rather than quadrate, and by the wings being paler. It is not likely to be mistaken for any other species.

The immense importance of the geographical distribution, bionomics, and breeding habits of *Glossina palpalis* has led to the accumulation of a large amount of detailed information on these subjects, particularly with regard to the precise localities in which the fly is found and to its seasonal prevalence in different areas. It will not be possible, within a reasonable space, to give even an abstract of the very numerous papers which have appeared within the last few years, nor is this necessary, as almost all have been adequately summarized as they appeared in the *Sleeping Sickness Bulletin* and its successor, the *Tropical Diseases Bulletin*, both of which are easy of access. In the following account no attempt is made to do more than set forth the main facts.

The area of distribution of this species, which corresponds more or less closely with the area in which Sleeping Sickness is endemic, extends throughout West and Central Africa. The northern boundary stretches

Geographical Distribution

from the mouth of the Senegal river (16° N.), to the district of Bhar-el-Ghazal, in the south of the Anglo-Egyptian Soudan. It extends southward as far as Angola on the west and to the southern borders of the Congo Free State. The eastern limits are formed by the valley of the Nile and the shores of Lake Victoria and Lake Tanganyika. It is not found in Eastern Africa, though some specimens were taken by Kirk on the Zambesi river in 1864. As Neave points out, this area closely coincides with the Western Equatorial region of zoologists, where the fauna is essentially tropical; in the Zambesi basin, which is cut off by the high plateau of the Congo-Zambesi watershed, the fauna is mainly South African. It will be noticed that the area of distribution corresponds to the region drained by the three great rivers, the Senegal, the Congo, and the Niger.

Neave has made some interesting observations on the distribution of this species, which have some bearing on the possibility of exterminating it by clearing the bush. He points out, for instance, that in the basin of the upper Nile and on the eastern shore of the Victoria Nyanza the distribution of the fly is remarkably discontinuous and erratic, and that in this region there is evidence that some climatic change is going on, resulting from an alteration of the watershed. The whole of the Kioga basin is now flat and traversed by swampy water courses, a type of country, which, as will be seen presently, is quite unsuitable to this species.

Habitat

The distribution of the fly within this area is by no means continuous, but is determined by certain remarkably constant and well-defined conditions, in the absence of which the nutritive and reproductive functions cannot proceed in a normal manner. These condition are, briefly, a high and constant temperature (about 28° C), a degree of humidity approaching saturation, abundant shade, and a suitable food supply.

Country presenting these features is to be found throughout the courses of the great rivers of Africa, and along the shores of the lakes, where the surface of the land is covered for the most part with dense forest and jungle. The species has not been found at an altitude of more than 4,000 feet, nor does it occur in areas from which, whether naturally or by the hand of man, the dense undergrowth and trees have been removed. In those districts in which the surface of the land is intersected by a network of small rivers and streams during the rainy season, but becomes dry in the dry season of the year, the fly exhibits a marked seasonal prevalence, disappearing as soon as the degree of humidity falls with the drying up of the water courses, even though the temperature is not in itself unfavourable, and though both shade and food supply are present. The shade necessary for the fly is that of dense forest, in which it is well protected from the direct rays of the sun, rather than that of thick shrubs and undergrowth near the ground; shade and moisture appear to be more important than a particular temperature, for a fall in the latter, though it delays the life processes, does not inhibit them or cause the fly to seek fresh quarters. An excess of moisture, such as occurs in large swamps, is also unfavourable, especially since in such situations the deep shade of forest trees is not usually available.

The food supply of *palpalis* is present almost everywhere, as this species is by no means restricted to any particular host or group of hosts. According to Roubaud *palpalis*, more than any other of the genus, is addicted to the blood of man, a most important fact in relation to the spread of Sleeping Sickness; but it will feed readily on almost any mammal, on domestic animals, cattle and pigs, on game of all kinds, and particularly on deer and antelope; birds, lizards and snakes, are also attacked, as has been definitely established by the presence of the characteristic blood corpuscles in the mid-gut of the fly. The food supply does not, therefore, act to any great extent as a factor in determining the distribution of the fly in the broad sense, though it is of some importance, as will be shown later, in determining the precise localities in which the majority of the individuals in any given habitat are found. It is probable, however, that in some cases the disappearance of the fly from a given area may be connected with the migration of the game.

It will be readily understood that such closely circumscribed conditions, which hold, in a greater or less degree, for all species of *Glossina*, will not be found uninterruptedly throughout a large area. The presence or absence of the flies is determined by the physical conditions of the country, and it is often the case that one locality is heavily infected, while another, not far distant, is practically free from it. It is this circumstance which gave rise to the term ' fly belt ', applied by the older travellers in Central Africa to regions infested with the ' tsetse fly ', (not necessarily *palpalis*), and so much dreaded by them on account of the inevitable loss of domestic and transport animals which occurred to those who had to traverse them. Such fly belts are not, of course, constant in position, but vary according to the seasonal nature of the rainfall and the migratory habits of the game.

Roubaud makes a useful distinction between those haunts of the fly (termed by him *gîtes*) which are permanent and those which are temporary, and divides these again into those in which the flies subsist mainly on human blood, and those in which the food is derived from other vertebrates, chiefly large game. In the permanent gîtes the necessary conditions for *palpalis* are present the whole year round, and in such places, although the cold weather retards the life processes a little and renders the flies less inclined to feed, and therefore less evident, they are met with uninterruptedly throughout the year. The necessary conditions are to be found along the shores of the large lakes, and along water courses which do not dry up in the dry season. Temporary gîtes, as already indicated, include the large tracts of country which are intersected with a network of small rivers and streams during and after the rainy season. It has been shown that the flies migrate from the permanent gîtes, which thus act as reservoirs, to the temporary ones, as soon as these latter become suitable, and again return as the water evaporates and the air becomes drier. *Palpalis* is never found far from rivers and streams, as it is only in their neighbourhood that the necessary degree of humidity is attained.

The localities described by Roubaud as human gîtes are of special interest on account of the close association which is shown between the fly and its host. Such haunts usually consist of comparatively small and sharply circumscribed areas, in which, in suitable weather, the flies are always to be found. In the case, for instance, of a permanent river flowing through forest country, the conditions are apparently favourable to the fly at all points, but it is found that the great majority of the individuals are collected together in those places where they are certain to meet with their human hosts at regular intervals, and are thus assured of a food supply. They are often, in fact, limited to the neighbourhood of fords, places where water is drawn by the inhabitants, or washing and bathing places, where they rest concealed in the foliage while digestion is taking place, to reappear when a fresh meal is required.

Habits

Notwithstanding that deep shade is an essential condition of their existence, the flies are most active and bite most freely in sunny weather. On dull days they prefer to rest among the trees, and few or none may be seen in places which they are known to frequent. This is a point of some importance, as one might be tempted to assume that they are absent in any locality in which they were looked for under these unfavourable conditions. The behaviour of the different individuals at the human gîtes referred to above is very peculiar and interesting. Several observers have noticed that those which rest on the outskirts of the gîte, at some little distance from the water, are much the most active, and immediately attack the first host which comes their way, taking a full meal at the first opportunity; those which are in the interior, near the water, are found resting on stones on the river bank, or on trees thrown across the water; they make no attempt to bite and merely rest in the sun as near the water as possible, flying up when disturbed, but returning with a remarkable persistence to the same place. Many of these in the interior of the gîte are males.

The length of flight of *palpalis* under ordinary circumstances is probably not great, as they show no tendency to leave their haunts, but rather wait there till their prey comes to them. There seems to be no doubt, however, that they will occasionally fly considerable distances over water to reach boats passing along the rivers, and at the time of their migration from the temporary gîtes to the permanent water courses long distances may be covered, in this case by a series of flights. They frequently follow native carriers for some distance away from water.

Reproduction

Reproduction, in all the species of *Glossina*, is larviparous in type. The reproductive tract of the female has already been described in Chapter II, where it was explained that the two ovaries function alternately, first one and then the other producing an ovum, and that the ovum passes down into the uterus, where the larva hatches and completes its growth. It is necessary to consider the phenomena of reproduction in some detail; as before, the main source of our information is the extremely interesting thesis of Roubaud.

Descent of the egg

The passage of the mature egg to the uterus, according to Roubaud, is determined by a special mechanism, possibly under the control of the nervous system of the fly, which under certain circumstances may bring about the retention of the egg in the ovary, even when mature. One of the determining conditions is the presence of spermatozoa as a result of copulation; if copulation has not taken place, as in female flies kept apart from the male from the time they hatch out, a mature egg is found engaged in the upper end of the common oviduct, but never actually in the uterus; the egg which should follow this may be in a much more advanced state of development than would be found in the normal condition. The reason for this retention is that the aperture through which the spermatozoa penetrate is placed at the anterior end of the egg, and that the walls of the uterus contract so closely around their contents, by virtue of the large amount of muscular tissue in the wall, that if the cavity were occupied the sperms would neither be able to reach to and penetrate the egg, nor would they be able to pass into the spermathecae to be in readiness to fertilize the next egg. It is therefore essential that copulation, which takes place only once in the life of the female, should be accomplished while the uterus is empty.

Unfavourable conditions of temperature or humidity may also affect the reproductive function, either by causing the retention of the ova within the oviduct, or by stopping their development.

Intra-uterine development

The egg, in the normal course of events, descends into the uterus on the second day after the birth of the larva which preceded it. On the fifth day the larva emerges, and thereafter grows rapidly, until on the ninth or tenth day it has attained its full development and is born. During this period it passes through three moults, as is the case in the larvae of most Diptera. The first takes place very early, soon after the birth of the larva from the egg; the second is later, and takes place when the larva has reached twice or more its initial size; the third takes place, as in oviparous Diptera, at the time of pupation. In the first two moults the integument is very soft and thin, and it is only in the last, when the larva is about to be exposed to the external air, that the cuticle assumes any considerable thickness. The larval skins are transformed into a black compact amorphous mass, accumulated during the life of the larva in the anterior and ventral portion of the uterus, and extruded after the birth.

The larva

The full grown larva is cylindrical in shape, but of constantly changing dimensions during the short period which elapses between its birth and pupation; it consists of thirteen segments (Roubaud), and measures from 6 to 7 mm. in length, the breadth when at rest being less than one-third the length. In colour it is white, or yellowish white, except at the posterior end, which is highly modified and of a jet black colour. The head, as one would expect from its mode of life, is very small and inconspicuous; the succeeding segments down to the twelvth, on the ventral surface of which a minute vestigial anus can be detected, resemble one another, and have a roughened integument. The last segment is highly modified, and presents an appearance which is peculiar to the flies of this genus; the anterior or annular portion is strongly chitinized and densely pigmented, and is marked by a number of longitudinal striations projecting backwards from this there is a pair of large processes, gently rounded in shape, and with a roughened or shagreened surface. These caudal protuberances oppose one another, and form the boundaries of a deep pit. Their internal surfaces are marked by two slight linear depressions, which divide the inner surface into three lobes, the whole structure corresponding, as Roubaud has pointed out, to suppressed stigmal plates. The true openings of the lateral tracheae are situated in the pit between the protuberances.

Internal structure of the larva

The internal structure of the larva is specially modified for its peculiar mode of life, especially as regards alimentation. The alimentary canal shows the usual divisions, but each of these is adapted for the exceptional conditions. The *pharynx*, which is situated at the extreme anterior end of the body, immediately behind the buccal orifice, forms the sucking organ. In its dorsal wall there is a stout median process, which projects freely into the cavity anteriorly, and forms a sort of tongue, composed of longitudinal muscles bilaterally arranged, and some transverse fibres. The opening of the cavity is directed towards, and is in close apposition with, the papilla on which the duct of the accessory glands opens, and the larva obtains its nourishment by actively sucking the secretion provided by the glands. The papilla, in fact, serves as a teat. The *oesophagus* is an exceedingly delicate tube, which passes through a ring of nervous tissue in the ordinary manner, ending in a small proventriculus. The *mid-gut* is very highly modified, both in its structure and in the part it plays in the metabolism of the insect. It consists of three parts, of which the first and last are simple and tubular, and are slightly convoluted. The middle portion, on the other hand, is dilated into a voluminous sac, occupying almost the entire space within the body cavity, and in life is always distended with the granular milky fluid obtained from the accessory glands. The walls of this sac are of great delicacy, and contain very little muscular tissue; they are lined by a single layer of cells which resemble, as Roubaud points out, those of the fat body rather than ordinary digestive cells, and are constantly loaded with globules which are probably of a fatty nature. In the tubular portions of the mid-gut these cells are columnar and project freely into the cavity of the organ, but in the middle distended part they are flattened by the pressure of the contents until they form a very thin lamina. The saccular part thus resembles an organ for the storage of food material rather than a digestive chamber.

The *hind-gut* presents an equally striking peculiarity, in that it is shut off from communication with the mid-gut and also from the exterior, and thus serves only as a receptacle for the secretion of the Malpighian tubes. It commences at the termination of the wide tubular third portion of the mid-gut, at which point it is shut off from the cavity in front of it by a tight constriction, and passes upwards on the dorsal surface of the sac, turning again downwards to end at the anus, immediately internal to which there is a second constriction. The four *Malpighian tubes*, which are arranged in two pairs, one of each pair being shorter than the other, enter the hind-gut immediately behind the first constriction. It is noteworthy that there are no salivary glands in the larva.

Pupation

Immediately after birth the larva crawls away to find a suitable place for pupation. It progresses actively by means of wave-like contractions of the body wall upon the fluid contents, and can undergo, in the passage of any obstacle, very remarkable changes in shape; on occasion the anterior part of the body is distended and used as a battering ram. In a very short time the larva finds some crevice or hollow, a slight fissure in the earth, or a clump of dead leaves or debris, which will afford it some shelter, and comes to rest, usually at a depth of an inch or so beneath the surface. Pupation then takes place without further movement, and within a half or three-quarters of an hour the change is completed. The *puparium* (Plate XLVI, fig. 12) resembles in general that of most Muscids, being oval in shape, and slightly broader in front than behind; at the posterior end there are the conspicuous caudal protuberances, the shape of which, and of the notch between them, afford a valuable means of distinguishing puparia belonging to different species (Austen). The puparium, when fully formed, is of a dark brown colour, and measures 6·5 mm. in length and 3·5 mm. in breadth.

Bagshawe, who was the first to find the puparia in nature, obtained them on the shore of a lake, usually about ten yards from the water, and not more than twenty-five yards away. They were lying from half an inch to a little more than an inch below the surface, in the shelter of banana plants, shrub, and undergrowth, and always in a dry and crumbling soil; they were sometimes found in crevices of rocks and at the roots of trees. Comparative dryness seems to be a favourable condition for them, and most of the localities in which they were found were such that rain water would be quickly drained off.

Fraser and Marshall found immense numbers of puparia on the main Islands of Sesse in Lake Nyanza, in dry sand on the shore about five to fifteen feet from the high water mark ; Marshall also found large numbers on the sandy shore of the mainland. From these observations it will be seen that the breeding grounds of *palpalis* may be very extensive, and although they only relate to the shores of a large body of water, there can be very little doubt that the fly must deposit its larvae in the sand on the banks of rivers and small streams where it is said to be so prevalent; it is more than extraordinary that information on this point is so deficient. The breeding grounds of *palpalis* and probably of all the Glossininae recall those of the genus *Stomoxys*; the latter often select the sand banks of streams and rivers for oviposition, the damp sand being best suited to the habits of the larvae.

Much more information is yet required as to exactly where and at what time of the day *palpalis* deposits its larvae, especially in the temporary gîtes of Roubaud. The subject is of the utmost importance in the fight against Sleeping Sickness.

The duration of the pupal state is from thirty-two to thirty-five days; it can be reduced experimentally by an increased temperature. The pupae possess greater powers of resistance to unfavourable conditions than the imagines, but cannot resist a temperature of 30° C. to 35° C. They do not survive prolonged immersion in water or damp earth.

Number of larvae produced

It has been determined by observations on captive flies that the average duration of the life of a female *Glossina palpalis* is about three months, during which period she gives birth to from eight to ten larvae, at intervals of from nine to ten days, once the reproductive functions have become established. The period of development of the first larva is a long one, and its birth may not take place for as long as three weeks or a month, on account of the undeveloped state of the nourishing glands, which are not then able to provide a sufficient supply of food. Once the function is established, however, the reproduction proceeds very regularly, provided the food supply is copious and constant, and that the external conditions remain favourable. The different seasons do not appear to affect the production of larvae to any considerable extent.

Abortion and intra-uterine nymphosis

The pregnancy of *Glossina palpalis*, in captivity at least, does not invariably proceed to a successful issue. In some cases, when the conditions are unfavourable, the larva is expelled prematurely, and before it is in a condition to pupate. This is especially liable to occur with flies captured and brought to the laboratory in an advanced condition of pregnancy; it is probably due to their endeavours to escape from their unaccustomed surroundings. It can also be brought about by excessive moisture. Its occurrence is an indication of the necessity for quiet and rest during this stage, and is in agreement with what is found in nature, that flies nearly ready to give birth to their larvae remain at rest in the deep shade, and are seldom seen on the wing. Abortion produces no ill effects on the parent.

Intra-uterine nymphosis, which always results in the death of both the fly and its offspring, may also occur in captive flies, and has been once observed by Roubaud in nature. The larva is unable to escape by its own efforts, even if the mother dies at the time when it is ready to emerge.

Gestation has a marked influence on the nutrition of the female. At the commencement of pregnancy, and immediately after the birth of a larva, the fly will feed readily and fill itself to its utmost capacity, but as gestation proceeds and the abdominal cavity becomes more and more distended food is partaken of less eagerly, until by the time the larva can be seen through the abdominal wall the fly cannot be induced to feed at all.

Effects of temperature and humidity

There is, perhaps, nothing more striking in the bionomics of *Glossina palpalis* than its high degree of susceptibility to slight changes in the temperature and humidity of the atmosphere. It can only survive and carry on its life processes in a normal manner in such conditions as are provided by the river banks and tropical forest glades which are its natural environment, and in order to keep it in captivity the corresponding atmospheric conditions must be realized. The closeness of its relations to its environment are well brought out in some experiments recorded by Roubaud. He found that at the ordinary temperature of his laboratory (26°C.) the female fly would feed only every third day, when the previous meal was entirely digested, and that it could not be induced to bite on the second; an hour's exposure to a temperature of 28°C., however, resulted in an unusual activity, and the fly fed at once when a host was offered to it. This is in agreement with the frequently made observation that the flies in nature will only bite during warm and sunny weather. The stimulating effect of increased temperature is only brought about within narrow limits, for if the flies are maintained at a temperature of 30°C. to 35°C. they die in three or four days. Roubaud concludes that the optimum temperature for nutrition appears to be about 28°C., with a variation from 26°C. to 30°C. Even if maintained at a temperature of 30°C., with an average humidity (70 per cent.), they will not survive.

The effect of humidity is shown more by their resistance to adverse conditions, such as starvation, than by any effect on nutrition. Roubaud performed a series of experiments with flies maintained at temperatures of 25° to 27°C., 30°C. constant, and 33°C. constant, with the air deprived of its moisture by dessication, normal, and at saturation point, and showed very clearly that dryness is very unfavourable to the life of the fly in an unfed condition. At a temperature of 26°C., for instance, the resistance of the flies to starvation, in an atmosphere saturated with water vapour, was seven to nine times greater than in normal air, and thirteen times greater than in dried air.

Similar results, though obtained from a rather small number of experiments, are recorded concerning the effect of heat and humidity on the reproductive process. A temperature of 30°C., maintained for ten hours each day, resulted in the birth of the larvae in eight days and four hours, instead of the normal nine days. If the pregnant fly were exposed to a temperature of 33° C. to 35° C., however, even under the same nocturnal conditions, gestation was totally inhibited. Saturation of the air with moisture had also the effect of inhibiting gestation, the egg remaining in the ovary when it should normally have passed into the uterus.

Glossina palpalis var. *wellmani*, Austen. According to Austen this variety is slightly smaller than the typical *G. palpalis*, and the antero-lateral markings take the form of blotches. Newstead has examined a large series of preparations of the genital armature of the males of *wellmani*, and has found it to be identical with that of typical examples of *G. palpalis*. He states that, in his opinion, these differences are not subspecific but merely varietal, and that the variety *wellmani* occurs, in company with the typical form, in various localities; in a good series every grade should be found.

Glossina calignea, Austen. A medium-sized dark species resembling *G. palpalis*. Thorax with dark brown markings as in *palpalis*, but usually more extensive. Abdomen, first segment cream buff with a dusky patch on each side; second to sixth segments sepia brown. Distinguished from *palpalis* by its browner colour, and larger size; lower segments of abdomen browner. Genital armature of male distinguished from that of the male *palpalis* by the length of the claw-like extension of the superior claspers; the inferior claspers are also much more gradually attenuated, forming a leg-like extension distally, which terminates in a foot-like process bearing three or four slender and long hairs. Length, according to Austen, male 8 to 8·5 mm.; female 9 to 10 mm.

Austen states that this species is so far only known from Southern

Nigeria; it appears to attack travellers while in canoes, especially during the month of May, in places where there is dense cover consisting of long grass and water plants. Its early stages are unknown.

Glossina tachinoides, Westwood. A darkish grey to brown species, the smallest of all the tsetse flies. Thorax olive grey to smoke grey, with longitudinal bands of the usual *Glossina* type. Abdomen ochraceous buff with brown markings; first segment with large circular brown spots at the lateral angles, not reaching the lower border; third to fifth segments inclusive with dark lateral bands not reaching the middle line or the lower borders, and leaving a buff longitudinal median stripe. The size of the fly and the character of the abdominal markings will enable the observer to distinguish it from all the other species of *Glossina*. Length, according to Austen, male 6 to 6·75 mm.; female 6·8 to 8·4 mm.

The male genitalia are almost identical with those of *palpalis*, but can be distinguished by the shape of the inferior claspers, the inner lateral margins of which are proximally produced and broadly rounded; the outer margins are rounded at their distal extremities and deeply hollowed out; the inner margin is like a foot in shape, and has one or two hairs on it.

According to Austen this species has a wide range in West Africa; it is also found in Senegal, the French Congo, The French Soudan, German East Africa and Southern Arabia. It does not occur in the Congo Free State, Uganda or the East African Protectorate.

Bionomics: early stages.

The habits of this species recall those of *G. palpalis*, though, according to Roubaud, it prefers more open country, and groves along small streams; in the rainy season it may be found far from any water. It readily feeds on man. Roubaud finds that in captivity larvae are deposited on an average every eight days, and that the pupal stage lasts from eight to thirty-five days, the duration depending on the temperature. The larva and puparium, according to Austen, have remarkably large and tumid anal protuberances; the stigmal cleft is similar in shape to that of *morsitans*, but much wider than that of *palpalis*.

Glossina maculata, Newstead. This species is represented at present by a single specimen, a female, and is of doubtful validity; Austen regards it as a specimen of *palpalis*, which has become spotted by some foreign matter. Newstead, on the contrary, has no doubt regarding its specific identity, and refutes the statement that the dusky spots are due to the attentions of some other flies which were in the same packet!

In any case it is a rare fly, and the discovery of the male must be awaited.

Glossina fuscipes, Newstead. Until quite recently this tsetse was believed to be a rare species. Newstead states that it is allied to *G. palpalis*, but is distinguished from it by its small size, by the uniformly dusky legs, and by the dusky grey thorax. It measures 7½ mm. and looks like a dwarfed specimen of *palpalis*. The genital armature of the male is similar to that of *palpalis* and *tachinoides*, but has, according to Newstead, a curious claw-like process at the distal extremity of the superior clasper. The type, a male, was taken by Dr. Shircore at Nimulien, the Nile Province of Uganda.

Dr. McConnell recently collected a number of specimens from the same district, and at first believed them to be *palpalis*, but on examining the male genitalia he found that the superior claspers of all the specimens had these curious claw-like processes. The same was found in other specimens collected from the shores of Lake Edward and Lake Victoria. Other observers have examined the genitalia of apparently typical specimens of *palpalis* from Uganda, and have found the same appearances, so that it seems that most, if not all, the specimens of *palpalis* from Uganda are in reality *fuscipes*, Newst. In all other respects than the claspers this fly appears to be similar to *palpalis* and Mr. Marshall considers that it is best to treat it as a local variety.

Glossina pallicera, Bigot. A medium sized light brown species very closely resembling a lightly coloured specimen of *calignea*. Thorax olive grey with the usual brown longitudinal bands. Abdomen sepia brown with a lighter median longitudinal band on the first segment. The third joint of the antenna has a fringe, both anteriorly and posteriorly, of long delicate yellowish hairs. It is a rare West African tsetse; Austen states that it is found from Sierra Leone to the French Congo. Graham encountered it at Ashanti, where it was very local in its distribution. Austen states that Graham found it in the bush, where it was basking in the sun on the upper surfaces of leaves; it does not appear to be an active biter. Its early stages are unknown.

Glossina fusca, Walker. A large dark brown, almost black-winged, species with long and slender palpi. Thorax mouse grey, with brown bands of the usual *Glossina* type. Abdomen dark brown, first segment paler, no distinct bands. This tsetse closely resembles another species, *nigrofusca*, Newst., but can be distinguished from it by the absence of long hairs on the third joint of the antenna. Austen gives the lengths of the sexes as follows:— male 9·6 to 11·6 mm.; female 10·5 to 11·8 mm.

According to Austen *fusca* is found from Sierra Leone to the Uganda Protectorate, but it does not appear to be distributed in any of the East African Protectorates, nor has it been recorded from Rhodesia.

Bionomics and Early Stages

Kinghorn states that it is found in the bush, and that its habits resemble those of *longipalpis*. It often bites late at night. Bagshawe found the puparia of this species in the dry bed of a stream in the vicinity of Lake Albert, in the Uganda Protectorate, and was able to hatch out one fly. Austen gives the length of the puparium as 8 mm., and states that it is very similar to that of ***brevipalpis***, Newst. It can, however, be distinguished from it by the depth and shape of the stigmal notch. In ***brevipalpis*** the notch is relatively wide and shallow, not unlike a wide V in shape, while in *fusca* it is narrower, deeper, and distinctly U-shaped.

Glossina nigrofusca, Newstead. A large dark species closely resembling *G. fusca*, especially the female. Thorax mouse grey with dark brown markings. Abdomen dark brown. It can be distinguished from *G. fusca* by the fringe of pale hairs on the anterior and posterior borders of the antenna; by the darker colour and darker hind tarsi in the male, and by the narrower lines on the thorax. The superior claspers of the male are very widely separated, and the inner margin is produced to form a stout tooth-like projection. The harpes have the larger process strongly serrated along the upper edge, and a long narrow posterior process. Length, according to Austen, male 12·4 mm.; female 12·2 mm. It is distributed from Ashanti to the Congo Free State. Its early stages are unknown.

Glossina brevipalpis, Newstead. A large species with pale wings. Thorax pale to dark, with obscure greyish brown longitudinal stripes. Abdomen dark brown; first segment paler than the others. Distinguished from *G. fusca* and *G. nigrofusca* by its more robust form, paler colour, and indefinite thoracic markings; by its shorter and stouter palps, by the great length of the median process of the male genital armature, and the form of the harpes, which have broadly dilated tips. Length, according to Austen, male 10·2 to 12 mm.; female 11 to 13·5 mm.

This tsetse has been confused with *fusca*, under which name it was described by Austen in his Monograph of the Tsetse Flies, in 1903; the *fusca* of Stulhmann and others is in reality ***brevipalpis***, Newst.

Austen states that ***brevipalpis*** is common in many parts of South, Central and East Africa, but is unknown in West Africa. It is very abundant at the north end of Lake Nyassa, in North Eastern Rhodesia and in German East Africa. Its occurrence in Rhodesia is of considerable importance, for it may yet be shown that it has something to do with the spread of human trypanosomiasis.

Bionomics and Early Stages

Stuhlmann has made the most complete study of this species. *Brevipalpis* is chiefly met with in thick bush, and nearly always in the vicinity of water. It is not uncommon to find it at high altitudes, as much as 3,000 feet above sea-level. It is an active fly and appears to feed at definite times, either in the early morning before 8 a.m., or in the evening from 4 p.m. In the interval it rests under leaves, on the barks of trees, and even on stones, always near the ground. Like many other species of *Glossina*, it prefers dark coloured animals and dark skins, and will bite through dark clothes.

Stuhlmann, who has studied its breeding habits in captivity, states that the larvae are dropped at intervals varying from ten to twenty-two days, and that in three months one female deposited eight larvae. In German East Africa it probably breeds throughout the year, though the wet weather appears to be somewhat unfavourable to the development of the pupae. The freshly extruded larva measures 9·1 mm. in length and 2·3 mm. in breadth. The puparium, according to Austen, is of the usual brown colour, and measures about 7·5 to 8 mm. in length; the duration of the pupal stage varies from thirty to sixty-five days, according to the temperature.

Glossina longipennis, Corti. A large light species, in size and general appearance resembling *brevipalpis*. Thorax greyish brown, with a narrow faint brown longitudinal stripe on either side of the median line; a pair of admedian pale brown spots on the suture, and four well defined dark brown oval spots in the form of a parallelogram, two in front and two behind the suture. Abdomen ochraceous buff, with dark brown marks on either side of each segment. This species can be distinguished from *brevipalpis* by the greater width of the front in both sexes; by the ocellar spot being dark brown, and by the thoracic markings. The harpes of the male genital armature are squamiform, the inferior claspers are small, and the tips overlap. Length, according to Austen, male 10·2 to 11·6 mm.; female 11·4 to 13 mm.

This is one of the most easily recognized of the tsetse flies; its characteristic colour, thoracic spots, and the well defined dark patch on the ventral surface of the bulb of the proboscis will prevent it from being confused with any of the other species. It is strictly an East African species, and has so far only been recorded from the East African Protectorate and Somaliland. Nothing much is known regarding its habits, except that it is said to come into railway carriages. Its early stages are unknown.

Glossina tabaniformis, Westwood. A large dark brown, dusky-winged tsetse, closely resembling *nigrofusca*. Thorax similar to that of *nigrofusca*, the dark markings more or less distinct; the abdomen also as in *nigrofusca*. Distinguished from it by the shorter palps, and shorter hairs on the posterior border of the third segment of the antenna. Distinguished also from *medicorum* (see below) by its slightly longer palps and by the structure of the harpes of the male, which are divided into four pointed processes. Length, according to Austen, male 10·4 mm.; female 10·25 to 10·8 mm. It is found along the Ivory and Gold Coasts, Southern Nigeria and the Congo Free State. Practically nothing is known about its habits or early stages.

Glossina medicorum, Austen. A medium sized to large species, with a superficial resemblance to *brevipalpis*. Thorax dark grey with the usual dark markings. Abdomen dark brown. Distinguished from *brevipalpis* by the wings, which are uniformly coloured in both sexes, and by the structure of the harpes of the male, which have one broadly lanceolate appendage. Length, according to Austen, male 9 to 10 mm.; female 10 to 10·6 mm. This species has so far only been found in West Africa. Its habits and early stages are unknown.

Glossina pallidipes, Austen. A medium sized or large species resembling *longipalpis*. Thorax grey or smoke grey, with the usual dark markings, but as a rule broken up or reduced. Second abdominal segment light brown, with a dark brown patch at the lateral border; third to the sixth segments inclusive with broad dark brown bands, as a rule ending abruptly near the centre, thus leaving a pale median stripe. Length, according to Austen, male 8·5 to 10·4 mm.; female 9·75 to 11·25 mm. *Pallidipes* can be distinguished from *morsitans* by the fringe of hairs on the third joint of the antenna, and by the shape of this joint.

G. pallidipes is for the most part found in Eastern Africa; Austen mentions Portuguese East Africa, Nyasaland, North Eastern Rhodesia, German East Africa, and the Uganda Protectorate as the approximate range of its distribution. Its occurrence on the Victoria Nile, near Masindi Port, in company with *morsitans*, has recently been reported by Neave, who also states that it is to be found in Southern Nyasaland; the exact localities are not given.

Bionomics and Early Stages

Neave states that this species is found in the type of country frequented by ***morsitans;*** it is not entirely confined to the banks of rivers, but is almost invariably associated with a large amount of bush, in low-lying river valleys. According to Neave it appears to have a seasonal prevalence in British South Africa, being most numerous during the wet season and the following months. The opening up of the country, and its cultivation, seem to have a marked effect in reducing the numbers of *pallidipes.* Very little is known regarding its early stages. Austen records the main characteristics of the puparium, which measures from 6·4 to 7 mm. The anal tubercles are separated by a wide U-shaped notch, not unlike that of the puparium of *fusca.*

Glossina longipalpis, Wiedemann. A large tsetse very closely resembling *pallidipes,* but distinguished from it by the brown tips to the last two joints of the front and middle tarsi, and the shape and structure of the superior claspers of the male. The differences in the structure of the external genitalia given by Newstead are as follows :—

	G. longipalpalis.	*G. pallidipes.*
Heel or posterior lateral tooth.	Outer lateral margin taking same contour as the margin of the clasper.	Outer lateral margin curved inwards.
Single long hair on distal margin.	Long and capable of overlapping corresponding hair on opposite clasper.	Short and not capable of overlapping hair on opposite clasper.
Inner flange-like extension of superior clasper.	Greatest breadth about one-fourth the width of the narrowest portion of the stem.	Breadth greater than the width of the narrowest portion of the stem.
Longest hairs of editum.	Equal in length to the superior clasper.	One-half the length of the superior clasper.

Austen gives the distribution of this West African species as extending from Senegal to the Katanga District in the Congo Free State.

Bionomics and Early Stages

Roubaud has studied the early stages of the fly, and finds that in parts of Dahomey it may be seen in bush country, whereas in Central Dahomey it is met with in the vicinity of rivers and streams. It is abundant during the rains, but almost disappears during the dry weather ; it chiefly feeds on game. In captivity the female deposits her larvae about every ten days ; the pupal stage lasts thirty-five days on the average.

Glossina morsitans, Westwood. (Plate LI, fig. 2). ‘A medium-sized light grey fly with a banded abdomen. Thorax light grey, with longitudinal markings reduced to streaks. Abdomen buff, with a brown spot at the lateral margins of the second segment; third to sixth segments inclusive with a brown transverse band, not reaching to the middle line. Antenna without a fringe of hairs. A distinctly marked fly, not likely to be mistaken for any other species.

Geographical Distribution

This species is widely distributed in Western and Central Africa, having a range considerably wider than that of *palpalis*. According to Austen it is found from Senegambia on the west coast (16 N.) to the southern part of Kordofan (12 N.); on the south it extends from Southern Abyssinia in a south-westerly direction to the Bechuanaland Protectorate, and is present in the northern part of Rhodesia. It is a common fly in most of the places in which it occurs, and is probably the one which was referred to by the older travellers as the 'tsetse', the presence of which in certain regions led to their being termed fly belts.

Relations to disease

As a cause of disease *morsitans* ranks next to *palpalis*. Long before the etiology of trypanosome diseases was understood the presence of this fly was associated, by natives of the country and European travellers alike, with Nagana, a fatal disease of domestic stock. It was Bruce's discovery that the trypanosome which is the causal agent in this disease is transmitted to the animals by the bite of the fly which directed attention to the genus in relation to human trypanosomiasis. Within the last year or two the species has come into prominence owing to its occurrence in areas in which, although *palpalis* was absent, cases of human trypanosomiasis were found. Its connection with Sleeping Sickness is now accepted as proved. Taute, working at Lake Tanganyika, has shown it to be capable of transmitting a human trypanosome, probably *T. gambiense*. More recently Kinghorn and Yorke, working in the Luanga valley, have conducted a series of experiments on the same lines as those which established the rôle of *palpalis*, and have shown that *morsitans* can transmit *T. rhodesiense* Stephens and Fantham, to monkeys and other animals. The species has thus come to have a very great importance in those regions, such as Rhodesia, in which cases of Sleeping Sickness have recently come to light, and in which *palpalis* does not occur.

Habitat and Habits

The kind of country frequented by this species is very different to that in which *palpalis* is found, and it is rare to find the two in the same locality, a fact which is not surprising in view of the very narrow limits within which the latter species can thrive. Whereas *palpalis* is restricted to the close neighbourhood of running water, where the degree of humidity is constantly high, and to the dense shade of forest trees, *morsitans* frequents less densely wooded country, and, though it occurs near water, is not nearly so closely associated with it. The type of country which it inhabits is defined by Neave as 'a combination of the presence of such vegetation as will 'provide moderate but not excessive cover, coupled with a hot and 'moderately or even dry climate.' Such conditions are to be found in thick scrub and brush, near isolated clumps of trees and thickets with dense undergrowth, rather than in the dense forests along the banks of the great rivers. It is found at a much higher elevation than is the case with *palpalis*, having been recorded at an altitude of 5,000 to 5,500 ft. on the Congo-Zambesi watershed.

In suitable localities the fly often occurs in enormous numbers, swarms of them attacking travellers and their animals. Like the others of the genus, it bites most actively in warm sunny weather, and is seldom seen on dull and cool days; the older travellers used to take advantage of its diurnal habits and to attempt to pass through the fly belts with their animals during the night. At times, however, it will bite at night, especially in moonlight and when the weather is warm. Almost any large animal will serve as host, and among them, of course, man, though this species does not appear to exhibit the predeliction for human blood which has been noticed in the case of *palpalis*. There is some reason to believe that the buffalo, in the days before it was decimated and dispersed by rinderpest, when it was the most numerous of the larger mammals, was the main food of the fly. The alteration in the distribution of the fly, and its disappearance from, and reappearance in, certain localities in South Africa, is attributed to the scattering of the game.

Reproduction

Until recently very little was known about the reproduction of this species, or regarding the places in which its puparia were to be found. One was discovered in 1910 by Mr. Jack between the roots of a tree on the bank of a river in Southern Rhodesia, and until the present year his find remained the only record. The Luanga Sleeping Sickness Commission, reference to the work of which has already been made in connection with their demonstration of the transmission of *T. rhodesiense* by means of this species, were more successful, and Lloyd, the entomologist to the Commission, records the finding of numerous puparia. The situations in which they were found emphasize the difference in the localities chosen by this fly and *palpalis*, and also suggest that the larva is possessed of very considerable powers of locomotion. Of the nineteen localities which are recorded, in sixteen the puparia were in close association with trees, either in hollows under recumbent branches or trunks, at the roots, or actually in hollows and crevices of the trunk itself; the height above ground was considerable, in one case as much as four feet. No particular species of tree appeared to be selected, the number including eight different kinds, but Lloyd notes that in all cases the trees were either abnormal or injured. In one case ten puparia and four empty cases were found in a cup which had been produced at the end of a looped branch by the rotting away of the soft wood within the bark. The majority of the puparia were in such positions that they must have been exposed for several hours each day to the direct rays of the sun; in one instance, of the nine living puparia and six empty cases which were found in the deserted burrow of an ant-bear, all were on the side which would catch the morning sun. The distance from water varied so much as to indicate that the species does not specially select the neighbourhood of a water course for the birth of the larva; some were found on the banks of streams, others at considerable distances away from water, in one case as much as half a mile.

Lloyd publishes some interesting observations on the duration of the pupal stage, which he shows to be influenced in a very distinct manner by the temperature. The shortest period noted was twenty-one days, the longest eighty-eight, the respective temperatures being 86° C. and 62° C., the seasons October and May. The extremes of temperature, however, were not favourable, and many of the flies which hatched out after long intervals were deformed and weak. Lloyd thinks that under natural conditions the periods would be less than in the laboratory, as the puparia would be warmed by the sun. It was found that when the flies were needed for experiments the pupal stage could be shortened artificially (during the cold weather) by keeping them warm.

The puparium of *morsitans* is smaller than that of *palpalis;* the anal protuberances, which are relatively small, are of uniform width, and are not constricted at the base.

Glossina severini, Newstead. A medium-sized species resembling somewhat *G. fuscipleuris.* Thorax robust, with the usual *Glossina* markings better defined than in *palpalis;* pleura dusky grey. Abdomen unicolourous. Coxae of hind legs grey or greyish buff; tips of front and middle tarsi black. Hind tarsi either entirely dark brown or with the first and second segments a little paler than the others. Genital armature very similar to that of *medicorum*; editum with very long marginal hairs; harpes rudimentary, short and narrow with the distal margin irregularly serrated. Length of male 10·3 mm. to 10·5 mm.

This species, recently described by Newstead, was taken in the Congo Free State at Lac Mouro (River La Larva). It is closely allied to *medicorum* but distinguished from it by the small harpes, the greater length of the marginal hairs of the editum and by the greater length of the lateral branches of the hairs of the arista.

Glossina submorsitans, Newstead. Closely allied to *morsitans*, and regarded by Austen as a form or race of the latter. Newstead considers it to be a distinct species, and states that it can be distinguished from *morsitans* by the clearer and more sharply defined abdominal bands; by the median light band on the third, fourth and fifth segments being equal and narrower than in *morsitans*; by the abdominal bands being rounded medially and tapering towards the lateral margin. It is found in Nigeria; nothing is known regarding its habits or early stages.

Glossina fuscipleuris, Austen. This dark tsetse is allied to *fusca*, but can be distinguished from it, according to Austen, by the dark grey colour of the pleurae, and the longer finer fringe of black hairs on the hind coxae. Newstead has recently studied the armature of the external genitalia of the male of this species and finds that it resembles that of *tabaniformis*. The distinguishing characters are as follows. The harpes have three processes instead of four as in *tabaniformis*; the great width and serrations of the proximal teeth; the extreme narrowness of the second pair, and the ribbon-like character of the third; the sclerite of the vesica is notably large.

This species is found in the forest region of the Congo Free State. Nothing is known regarding its habits or early stages.

Glossina austeni, Newstead. A small slender species of the *morsitans* group. Its abdomen is of a bright ochraceous colour; the head is somewhat narrow. It may be confused with the other small tsetse fly *tachinoides*; it can, however, be distinguished by its small size, narrow head, bilaterally striped thorax, reddish abdomen and dark hind tarsi. According to Newstead, the foot-like shape of the superior clasper, and the narrowly pointed distal portion of the harpes, are characteristic.

Neave states that it may be mistaken for a small tabanid. It is found in the forest along the coast line of British East Africa in company with *pallidipes* and *brevipalpis*.

Breeding Technique.

From what has been said above regarding the early stages of the various species, the worker will have some idea where to look for the puparia; much has yet to be learnt regarding the larviposition of the tsetse flies. Once having found these breeding grounds, large numbers of puparia can be collected;

African boys employed in field laboratories excel in this work and make quite a lucrative living out of it. The puparia on being brought to the laboratory should be placed in glass jars, similar to those used in breeding the Muscidae (see page 343 and Plate XLIV, fig. 5); or in small boxes, such as the one devised by Bruce.

Kleine, who has given a complete account of his methods of breeding *Glossina palpalis*, always used large specimen jars, 8·5 cm. in height and 6·5 cm. in width. All observers who have used tsetse flies for transmission experiments have abandoned the earlier methods of keeping the flies in large airy wooden cages with moist grass, rocks and other natural objects; the flies do not thrive in them, and are very difficult to control. Ants and other laboratory pests soon make their way into the cages and destroy the flies.

In keeping *palpalis* in his fly jars, Kleine takes the precaution of covering the top with a fairly wide-meshed mosquito net, the meshes being just narrow enough to prevent the deposited larvae from crawling out. He points out that the jars must be kept scrupulously clean, and that the flies must be regularly fed; the feeding, though carried out by the African boys, must be under the control of one of the members of the laboratory. The flies are fed daily, often twice a day, on sheep and goats. The animal is first tied down, the side of the abdomen then shaved over a large area, and the jar is inverted over it without exerting any pressure; it is kept like this until all the flies have fed. This may occupy a considerable time, as some flies are very slow in finding a suitable spot.

As a rule Kleine kept three flies in each jar, two females and one male, but never more than five; if too many are placed together they are apt to become damaged by a deposit of faeces on their wings and bodies. Kleine lined the bottom of the jars with several layers of filter paper, which soaked up most of the liquid faeces. The flies should never be fed on unhealthy or anaemic animals, or on cold-blooded animals.* The feeding experiment should not be begun till the temperature is warm. The flies will suck blood on the first day after hatching, but do not feed actively till after the second. The jars should be changed daily and if possible twice a day, and great care should be taken that the fresh jar is absolutely dry. The changing of the flies from one jar to another is accomplished in the following way:—The clean jar is placed on a table and the one containing the flies inverted over it, so that the mouths of the two are in perfect contact; the mosquito netting is then untied and partially drawn out and the top jar tapped, when the flies will pass into the lower one. The netting is now replaced and tied round the mouth of the fresh jar, and the old one removed. This little manoeuvre is soon learned, and if care is taken the flies do not escape. The jars must be carefully labelled and always returned to the same place. Kleine kept his jars on a table divided up into compartments, each of which was covered with a cloth; the jars were all laid on their sides. The puparia can be readily recovered from the jars by opening the netting opposite the place where they are lying, tilting the jar, and gently rolling them on to the palm of the hand; if any of the larvae escape out of the jars they will be found on the cloth on the floor of the compartment.

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* Lloyd notes that when *morsitans* was fed on fowls, the blood forms a hard clot in the crop.

The puparia are transferred to larger jars, on the bottom of which there are layers of sand, and are buried just beneath the surface, the mouth of each jar being covered with mosquito netting. Puparia can be carried long distances by packing them in a small box with some sand, taking care not to have too much sand over them, otherwise they are apt to be suffocated.

From the twentieth day onwards the puparia should be examined daily. The recently hatched flies are removed from the pupal jar by the same method as that employed in changing the flies from one jar to another. If all the above precautions are observed, and the feeding and keeping of the flies carefully supervised, they can be kept alive for months.

When experimenting with caught tsetse flies the worker should bear in mind that they may be naturally infected with protozoal parasites (gregarines and flagellates). Novy was the first to recognize the importance of the natural flagellate (*Crithidia grayi*) of *Glossina palpalis.* Since he pointed out the possibility of confusing this parasite with the developmental stages of any trypanosome the fly may ingest, several observers have attempted, but without success, to shew that *grayi* is a vertebrate trypanosome. Minchin for instance believed *grayi* was a bird trypanosome, while Koch and Kleine were of the opinion that it came from the blood of the crocodile. In discussing this subject one of the writers pointed out that there is no proof that *grayi* is a vertebrate trypanosome, and that it is in all probability a natural flagellate of *Glossina palpalis.* Roubaud has recently attacked this problem. After examining a large number of flies, and finding that *grayi* cannot be inoculated into animals in any of its invertebrate forms, he comes to the conclusion that there can be no doubt that it is a natural flagellate of the fly. It has yet to be shewn how *palpalis* becomes infected and whether *grayi* represents one or two distinct species.

CHAPTER IV

SECTION 2

THE ORDER DIPTERA; THE PUPIPARA

Small to moderately large flies, with integument of a leathery consistence. All the species are ectoparasites of warm-blooded vertebrates. The eggs hatch out in the body of the female fly and the larvae are nourished by special glands, and when fully mature are deposited on the ground or in the abodes of their hosts.

The Pupipara represent a remarkable group of flies whose structure has become greatly modified in accordance with their parasitic habits; unlike other Diptera, they cling to their hosts, crawling in between hairs or feathers. Those forms with wings never fly long distances, but merely use them to pass from one part of the body of the host to another, or to fly from one host to another close by. In some species, though the wings are well developed at one stage, they are subsequently shed; in others they are either rudimentary or entirely wanting. The legs, on the other hand, are highly developed; they may be short and stout, or long and slender; the claws are always specially adapted for clinging and may be denticulated and armed with accessory spurs. Their bodies are more or less compressed dorso-ventrally, a modification well adapted to their parasitic habits; they are often furnished with spines and ctenidia. The abdomen is as a rule indistinctly segmented and of a leathery consistence. Except for *Braula coeca*, which is a minute insect living on bees, all the species feed on the blood of their hosts.

WILLISTON'S KEY TO THE FAMILIES OF THE PUPIPARA

1.	Wingless flies, parasitic upon bats; head folding back on the dorsum of the thorax	**Nycteribiidae.**
	Winged or wingless flies, parasitic on birds or mammals; head not folded back upon dorsum of thorax	2
2.	Antennae reduced; wings with distinct parallel veins and outer cross-veins when present; claws simple; palpi leaf-like, projecting in front of the head; almost exclusively parasitic on bats	**Streblidae.**
	Antennae usually more elongate, the joints more or less distinctly separated; head sunk into an emargination of the	

thorax; wings, when present, with veins more or less crowded anteriorly, the weaker ones running outward and backward, the cross-veins short and approximated to the base of the wing; claws large, bidentate or tridentate; palpi not leaf-like, nor protruding in front of the head . . . **Hippoboscidae.**

Speiser recognizes another family, the Ascodipteridae, which contains the single genus *Ascodipteron* with three species, *A. lophotes*, Mont., *A. siamense*, Speis., and *A. phyllorhinae*, Adensamer. These flies are all parasitic on bats and are usually found buried in the skin of the host's wing; they are extremely aberrant forms with unsegmented bodies and without any apparent head.

FAMILY HIPPOBOSCIDAE

Leathery flies with relatively large wings closed cross-wise, completely concealing the abdomen. Head flattened; eyes round or oval, with or without ocelli. Palpi ensheathing the proboscis. Antenna with one joint inserted into a depression and usually armed with spines or long hairs. Thorax flattened and horny, with yellowish spots; scutellum short and broad; halteres small and often rudimentary. Abdomen sac-like, of leathery consistence; segmentation indistinct or entinely absent. Legs short and broad, all segments well developed; tarsi short; claws strong, and often with one or more spurs. Wings present or absent; when present the veins are crowded together towards the anterior border, a few weak ones extending obliquely across the wing membrane.

All the species are parasitic on mammals and birds. They behave in a characteristic manner when disturbed, making short rapid flights, and alighting on some other part of the host, quickly burying themselves in the hair or among the feathers. Several species may be encountered on recently killed game, and on raptorial birds.

Speiser recognizes the following subfamilies and genera:

1. SUBFAMILY OLFERSIINAE. Hippoboscidae in which the wing is well developed, and the anal cell is absent; the pronotum is visible from above; ocelli are absent. Genera:—*Ortholfersia, Olfersia, Lynchia, Icosta* and *Pseudolfersia*.

The important genera may be recognized with the aid of the following key:—

1. Wings lanceolate, rounded at the tip; scutellum truncate . **Lynchia.**
Wings of usual shape; scutellum not truncate 2

2. Distance of oral border from frontal suture as great as from the suture to the vertex . . . . **Pseudolfersia**
Distance from oral border to suture distinctly less than from the suture to the vertex . . . . **Olfersia.**

2. SUBFAMILY HIPPOBOSCINAE. Hippoboscidae in which the wing is well developed and the anal cell is absent; the pronotum is visible from above as a projecting coloured ring; ocelli are wanting. Genus. *Hippobosca*.

3. SUBFAMILY ALLOBOSCINAE Hippoboscidae with rudimentary wings in which the anal vein is so far developed so as to appear retroflexed and to enclose an anal cell; ocelli absent. Genus *Allobosca*.

4. SUBFAMILY LIPOPTENINAE. Hippoboscidae some of which have weak wings with reduced veins; most either with wings shredded or consisting of mere tags; ocelli present or absent. Genera *Lipoptena*, *Echystepus* and *Melophagus*.

The two important genera are distinguished as follows:—

1. Wings present, but as a rule becoming detached in the female; ocelli present . . . . **Lipoptena.**
Wings and halteres entirely wanting . . . . . . **Melophagus.**

5. SUBFAMILY ORNITHOMYNAE. Hippoboscidae with either developed or reduced wings; in the former case usually with an anal cell. Ocelli may be present or absent; those with an anal cell have ocelli; others again have no distinct venation. Genera:—*Ornithoeca*, *Ornithomyia*, *Stenopteryx Ornithoctona*, *Ornithopertha*, *Ornithophila*, *Caetacrhina*, *Myiphthiria Brachypteromyia*, and *Stilbometopa*.

The important genera can be distinguished as follows:—

1. Claws with an accessory tooth 2
Claws simple, without any accessory tooth between the basal plate and the tip 3

2.	Ocelli present	**Ornithomyia, Ornithopertha and Ornithoctena.**
	Ocelli absent	**Stilbometopa.**
3.	Anal cell present	4
	Anal cell absent	**Ornithophila.**
4.	Ocelli present; wings narrow and about ten times as long as broad	**Sternopteryx.**
	Ocelli absent; wings only about three times as long as broad	5
5.	Wings about as long, or little longer than the abdomen	**Oxypterum.**
	Wings rudimentary and shorter than the abdomen	6
6.	Wings with distinct veins. Asiatic species	**Myiophthiria.**
	Wings with indistinct veins. North American species	**Brachyteromyia.**

GENUS LYNCHIA, WEYENBERG

The hippoboscids belonging to this genus are parasitic on birds; some ten species are recorded from the Mediterranean region, Madagascar, the Canary Islands, and South America. *Lynchia maura*, Bigot, is a common parasite of pigeons, and is found all along the shores of the Mediterranean and in parts of South America. It was in this fly that the Sergents observed the development of *Haemoproteus* (*Halteridium*) *columbae*, having previously failed to find any development in *Culex pipiens*. In Brazil, Beaurepaire Aragao has recorded the development of the halteridium of the pigeon in *Lynchia brunea lividocolor*. His observations, together with those of the Sergents, strongly suggest that this blood parasite does not pass through a typanosome stage in its invertebrate host.

GENUS HIPPOBOSCA, L.

Head flattened, both sexes dichoptic. The thorax is nearly always of a yellowish or reddish brown colour, and is marked with spots or bands. Abdomen sac-like and without distinct segments. Wings in the resting position crossed and completely covering the abdomen.

The flies of this genus are often spoken of as horse flies, a term which is better applied to the Tabanidae. With one exception, *Hippobosca struthionis*, Jan., all the species are parasitic on mammals. It is sometimes difficult to recognize the sexes; the female always has a small chitinous flap at the dorsal end of the abdomen, while in the male there is a small chitinous spine in the same situation.

Hippobosca maculata, Leach, (Plate LII, fig. 1) is common on cattle and horses; in India it is often seen in large numbers on draught cattle, resting about the scrotum. *H. struthionis* is found on the ostrich, clinging to the skin under its wings and tail. Some years ago it proved a serious pest in the ostrich farms in Cape Colony; it was extremely prevalent, and if not removed led to considerable deterioration of the feathers of the birds.

The Puparium
Plate XLVI, fig. 13

The female *Hippobosca* will readily deposit her larva in captivity, but unfortunately it is very difficult to keep the flies alive in cages, and pupae can only be obtained from those which are sufficiently far advanced in gestation at the time of capture to survive until delivery. Many of the larvae of captive flies appear to be deposited prematurely, and do not survive.

When first deposited the larva is yellowish white with a black cap; it is not capable of any movement. It slowly darkens and the puparium then resembles a seed. The puparium of *H. maculata* is oval in shape, with the anterior end somewhat flattened and the posterior extremity truncated. Austen describes its structure as follows:— 'The puparium 'examined is 4·4 mm. in length, by 3·8 mm. in breadth at the 'widest part, and 2 mm. in breadth at the posterior extremity. Rather 'less than 1 mm. in front of the posterior extremity the pupa-'case is encircled by a shallow groove, marking off a terminal area '(corresponding to the "black cap" of the larva) which, by means of 'a Y-shaped groove of little depth, is distinctly divided into three 'sections. At the apex of the median triangular section can be seen 'the vestiges of the posterior stigmata of the larva; the three sections, 'with the exception of a narrow vertical stripe in the centre of 'the triangular one, are covered with low tubercles. On the ven-'tral side in the median line, immediately in front of the groove, marking 'off the terminal area, is a small pore representing the larval anus. At 'a distance of 1·5 mm., behind the anterior and wider extremity 'the puparium is encircled by a second shallow and narrow groove, 'marking the limits of the cap that is split off when the imago 'makes its escape. On each side about 5 mm., from the lateral margin, 'on both dorsal and ventral surfaces, commencing immediately be-'hind this groove and extending back to a point about 8 mm. from 'the posterior groove, is a series of sharply marked punctures; those 'in each series on the ventral surface are connected by a deep furrow, 'which is less distinct on the dorsal side. In the specimen examined, 'there appear to be seven punctures in each dorsal row, and six in 'each row on the ventral surface.'

It is believed that the females of the genus *Hippobosca* deposit their larvae on the ground, but it is not definitely known whether

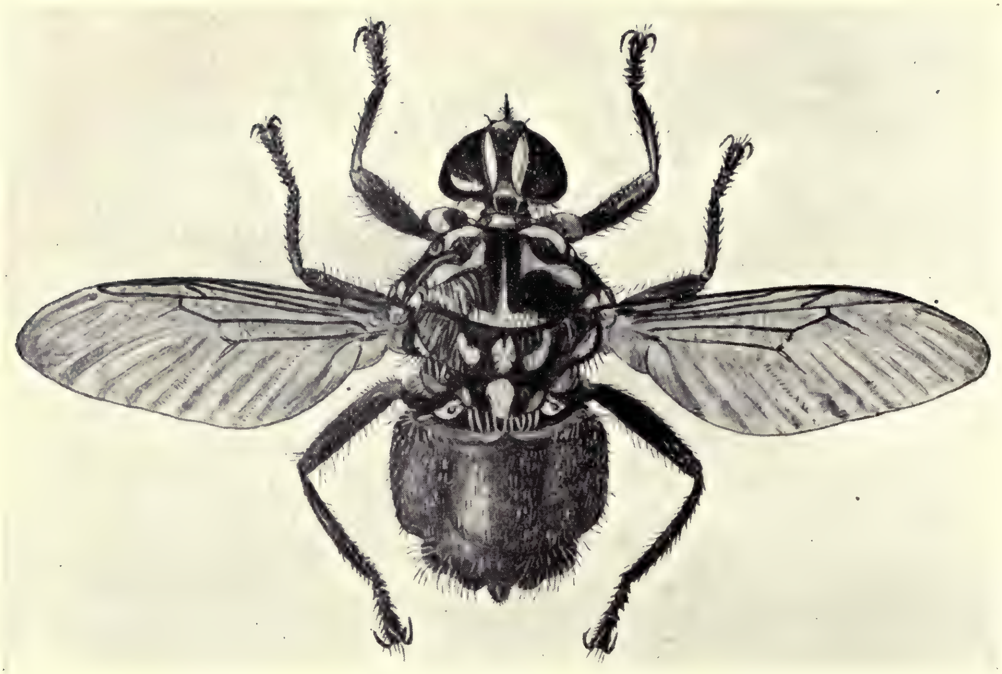


Fig. 1. Hippobosca maculata, ♀. × 8.

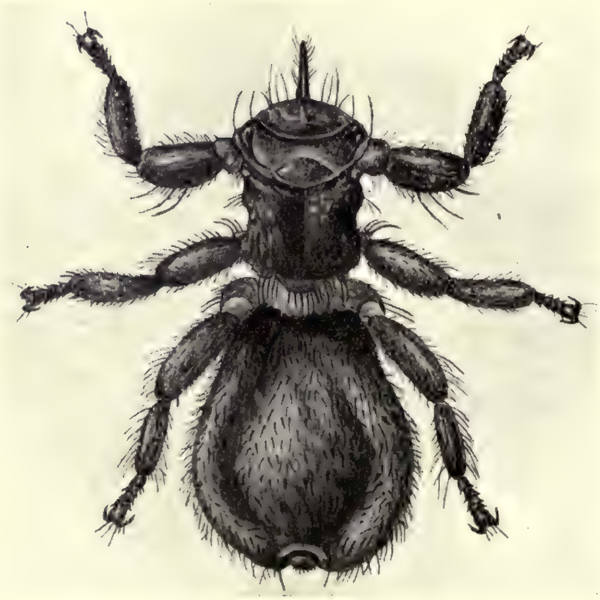


Fig. 2. Melophagus ovinus, ♀. × 12.

they bury them or merely place them on the surface. Several puparia of *Hippobosca maculata* have been found in the calf sheds of the King Institute, but it is not clear as to whether they were intentionally or accidentally deposited there.

GENUS LIPOPTENA, NITZSCH

Resembling Hippobosca but distinguished by the presence of three ocelli.

The flies of this genus are parasitic on deer. *Lipoptena cervi,* L., a common European species, is parasitic on a large number of different kinds of deer. As usually seen the female is apterous, and it simulates *Melophagus ovinus* (see below); the presence of wing stumps will, however, help to distinguish it from the 'sheep ked'. The male *Lipoptena* usually has wings, more especially during the autumn months; Austen points out that the winged males differ from the apterous males in having the abdomen slender, and are of a paler colour. Brumpt has bred several species from the puparia and finds that both sexes possess wings when they emerge; on finding a host the wings of the female always break off close to their bases.

GENUS MELOPHAGUS, LATRIELLE

This genus contains three species, of which *Melophagus ovinus,* L., the 'sheep tick', 'louse' or 'ked' is the best known.

Melophagus ovinus, L. (Plate LII, fig. 2.) Head short and broad, fitting closely into the concave anterior end of the thorax; laterally it is protected by the coxae of the anterior pair of legs. The proboscis is long and well developed, but is concealed by the palps; the front is broader than long and the vertex is nude. The antennae are not very distinct; the eyes are linear, and ocelli are wanting. The thorax is short and flattened; scutellum rudimentary. Wing prominence distinct; halteres wanting. Abdomen well developed and usually a little more than twice as long as the thorax; segmentation not visible. Legs strong and covered with hairs; claws simple.

This small apterous fly is as widely distributed as its host, with which it has doubtless been carried all over the world. It is nearly always infected with *Crithidia melophaga,* Flu.; this true crithidia is of peculiar interest, as it is one of the best-known examples of a flagellate which is transmitted hereditarily. Its life history has been carefully studied by Porter, Swingle, and Flu.

FAMILY NYCTERIBIIDAE

Head somewhat oval and when at rest folded back into a groove on the dorsum of the thorax; antennae short consisting of two segments, the terminal one oval with bristles inserted on tubercles. Eyes and ocelli when present rudimentary. Thorax depressed laterally; a fan-shaped comb of bristles, the ctenidia, inserted in a hollow at the anterior end of the thorax. Abdomen in the female weakly chitinised; in the male the dorsal and ventral plates are well developed; there is usually a row of strong bristles on the ventral border of the first segment. Legs long; femora broad, tibiae club-shaped and metatarsi very long or short.

The flies belonging to this family are extremely aberrant. All the species are apterous, and on account of their general appearance are commonly called 'Spider flies'. All are parasitic on bats. They may be recognized by the spider-like manner in which they run over the body of the bat when it is handled. Practically nothing is known regarding their methods of reproduction. According to Chatton a species of *Cyclopoda, C. sykesi* is infected with *Crithidia nycteribiae.* The family is widely distributed.

SPEISER'S KEY TO THE GENERA

1. First ventral segment without ctenidia; all the metatarsi are short, as long as the three following segments together. The dorsal head wall is arched like a hood over the mouth parts and antennae . . . . **Archinycteribia**.
First ventral segment with ctenidia; all the metatarsi more or less elongated, only a little shorter to a little longer than the tibiae, and for the most part much longer than the tarsal segments taken together. The dorsal head wall is not arched over the mouth parts and antennae 2
2. The tibiae are not ringed and have on their ventral edge near the distal end three rows of strong bristles. The anterior coxae are seldom longer than broad 3
Tibiae with two or three clear rings 4
3. Head with eyes and one ocellus. Abdomen and legs with long brush-like bristles . . . . **Penicillidia**.
Head without eyes. Bristles never brush-like . . . . **Nycteribia**.
4. Tibiae with three rings. Eyes and two ocelli . . . **Cyclopodia**.
Tibiae with two rings. Eyes but no ocelli . . . . **Eucampsipodia**.

FAMILY STREBLIDAE

Head of moderate size, not flexed on the dorsum of thorax; neck freely moveable. Eyes when present small; ocelli wanting. Antennae two-jointed, inserted in pits; second segment with one or more bristles. Palpi *broader than long, projecting leaf-like in front of the head and not forming a sheath for the proboscis. Abdomen with a distinct basal segment and characteristic bristles; the remaining segments indistinct. Coxae of hind legs enlarged; all fifth tarsal segments elongated and enlarged. Claws not distinctly toothed; pulvilli present. Wings either wanting or rudimentary.*

All the species belonging to this family, with one exception, are parasitic on bats; their life histories are unknown.

WILLISTON'S KEY TO THE NORTH AMERICAN GENERA

1.	Wings functional, with six longitudinal and nearly parallel veins and three outer cross-veins	2
	Wings vestigial or wanting, not functional	3
2.	Thorax distinctly longer than broad; abdomen distinctly segmented, with two large proximal and three small distal segments; last tarsal joint not remarkably thickened	**Strebla.**
	Thorax rounded, but little or not at all longer than broad; abdomen usually indistinctly segmented; last tarsal joint thickened and elongate	**Trichobius.**
3.	Legs of usual length	**Aspidoptera.**
	Hind legs greatly elongated, twice the length of the body	**Megistopoda.**

THE COLLECTION AND PRESERVATION OF THE BLOOD-SUCKING DIPTERA

The only way to collect the blood-sucking diptera in large numbers is to take advantage of their feeding habits; searching for them in their resting places takes up a lot of time. A tame animal, that is, one which will allow the collector to manipulate a glass tube on its skin, and will stand the whisking of a fly-net near it, is practically invaluable. One of the authors has for many years used for this purpose a white cow, now so well trained that one can sit down beside her and watch a fly feeding through a pocket lens. In course of time all the blood-sucking Diptera in the neighbourhood have been taken from this host. The use of such a trained animal is of course not practicable when one is moving from place to place, but for those settled in a laboratory it is such a great advantage, and such a saving of time, that it is well worth the initial trouble and cost. Animals ordinarily regarded as 'very tame' by their owners are as a rule no use for the purpose, as they resent the too close attention of the collector. Failing a horse or cow which will stay quiet while grazing, the next best host to collect from is one in harness, as its movements are then to a certain extent impeded. It is always advisable to catch a large number of each species when one has the opportunity, in order to be able to study individual variations if this subsequently proves to be necessary, and to have a surplus for exchange. Duplicates are always welcomed at the various Schools of Tropical Medicine and at many Museums. Particular care should be taken to note the flies which feed on the different hosts, even if they are not to be collected. The determination of the common host or hosts of blood-sucking flies, the sites at which they usually bite, and the circumstances under which they will feed on other animals, have been much neglected.

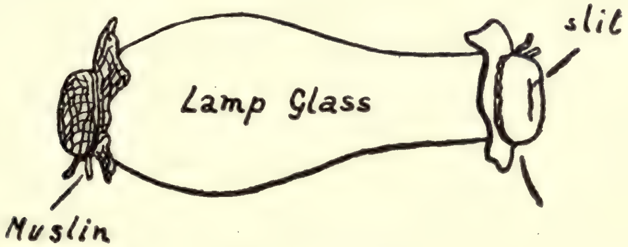
Apparatus for collecting Diptera. The Net

All that is required in the way of apparatus is a small net, some collecting tubes, a killing bottle, some pins, a pair of stout bent forceps and a small collecting box. If one is working within reach of a laboratory a net and some test tubes will suffice. A simple form of net made in the following way is recommended:—A stout piece of wire—telegraph wire does very well—about two feet long is bent into a circle about six inches in diameter, or considerably smaller for delicate flies, the remainder of the wire being turned into a handle by twisting the two ends around one another. On to this ring is stitched a muslin bag one and a half to two feet long, care being taken to see that the seams are on the outside, otherwise small flies will get caught in them. One should have spare bags in case the one in use becomes dirty or torn; it is only the work of a few minutes to stitch on a new one. If a longer net is required in order to catch flies resting out of reach, the handle can be tied to a stick. The elaborate and expensive folding nets sold by dealers in entomological outfits are not much use, as they are both too big and too heavy for catching active Diptera; they very quickly get out of order.

Collecting tubes

When the specimen has been netted, it should be driven to the bottom of the bag by a sharp turn of the handle, and then, if it is very active, it may be isolated in a part of the net with one hand; with the other a tube is passed in and the mouth placed over the fly. Less powerful flies can be readily transferred to a tube by inverting the mouth over them. The flies may either be collected in small tubes and killed in the laboratory, or they may be killed at once in the killing bottle. For collecting tubes, the most useful are small specimen tubes, 1 × 3 in. or a little larger. The mouth should be closed by a plug of cotton wool, never by a cork; neglect of this point will result in the early death and probable moistening of the specimens, especially on hot days. Larger tubes are useful for catching flies without the aid of a net; the large test tubes used in laboratories for cultivating bacteria on potatoes are very suitable for this purpose.

To catch a fly when it settles on the skin of a host, stand near it for a minute or so till it becomes accustomed to your presence. Then slowly approach it with a large tube, and hold this over it for a few seconds at a distance of a foot or so, till the fly gets accustomed to it. Then bring it very slowly nearer, till within striking distance, and then put the mouth of the tube over the fly as rapidly as possible. If this fails, use the net, whisking it over the fly with a rapid turn. It is as a rule unnecessary to touch the skin of the animal, for the fly is caught as it rises. *Hippobosca* is sometimes difficult to catch, and in this case it is best to have an assistant standing on the other side of the animal; the fly is thus kept moving from place to place and can then usually be caught with the hand or a net.



TEXT FIGURE 1

Colonel Adie, I.M.S., recommends the following simple method of catching mosquitoes; it is equally applicable in the case of other small flies. An ordinary long test tube is taken, and either three holes are drilled in it with a writing diamond, or the tube is drawn out in a blowpipe flame to a small bore, just too small to allow the fly to escape. The flies are caught in the ordinary way by placing the mouth of the tube over them, and are then transferred to a lamp chimney (Text fig. 1), the broad end of which is closed with a piece of muslin with a fine mesh, the narrow end by a piece of rubber tubing from an old bicycle tyre, in which a central slit is made. When the mosquito or other small fly is caught in the test tube, the mouth is thrust through the slit, and the fly blown through into the chimney by placing the mouth over the pierced or drawn out end; the opening in the rubber closes automatically when the mouth of the tube is withdrawn. In this way a large number of flies can be collected with the minimum amount of apparatus and trouble. The method is especially useful for native collectors, who are not required to discriminate between species.

Many small diptera, such as *Phlebotomus*, *Ceratopogon* and *Culicoides* can be caught around a strong light, such as that thrown on a white sheet by an acetylene bicycle lamp; the flies can be readily caught as they settle on the sheet. An electric light placed under a bell jar in the open attracts small flies in large numbers.

Killing Bottle

The killing bottle is prepared in the following way:—A wide necked bottle with a good stopper is selected; about a quarter of an inch of dry plaster of Paris is placed at the bottom, and over this a layer of powdered cyanide of potassium, or simply a few lumps. A layer of plaster of Paris and water of the consistency of thick cream is then poured on the top and allowed to set. In preparing the cream, always add the plaster to the water and not *vice versa*, or it will become lumpy. When the superficial layer of plaster has set, place two or three pieces of filter paper on it in order to absorb the moisture. This is especially important in the tropics, and neglect of this precaution will result in many of the flies becoming moist and their wings will adhere to the glass. When not in use the stopper should always be placed in the bottle. If the smell of the cyanide becomes weak, scratching the surface of the plaster often restores it.

Flies for museum specimens should always be killed and pinned as soon as possible, as if kept in the tubes they are apt to damage themselves, or to foul their wings and bodies with excreta. Those in tubes may be killed either by transferring them to the killing bottle, or by dropping chloroform or ether on to the cotton wool which is used as a plug. These fluids should on no account be dropped into the tubes, or they will alter the colours of the specimens.

Pins

The following size of pins are the most useful. No. 0, and No. 20 for all small species, such as *Ceratopogon*, *Culicoides* and *Phlebotomus*, etc., and for the smaller muscids. Nos. 3, 5 or 7 are best for such flies as *Tabanus* and *Glossina*. No. 16 is very useful for pinning the card or pith to which the fly is attached. Very long and delicate pins are sometimes used and with them a collection has perhaps a better appearance, but they require very careful handling, as they bend easily when thrust into the cork, and have to be manipulated with forceps, grasping the pin below the specimen. The pins should be lacquered, as this prevents the formation of verdigris at the point where it enters and leaves the body of the fly.

Pinning and Mounting

To pin a fly proceed as follows:—Place the specimen on a piece of cork mat and grasp it gently by the legs between the forefinger and thumb of the left hand. Then insert the pin, either with forceps or the fingers, through the dorsum of the thorax just behind the suture, and a little to one side of the middle line, pushing it well through and taking particular care that the point does not pass through any of the joints of the legs, or they may come off. The pin should be passed through the fly until it is about the junction of the upper and middle third of the pin. Some specimens should also be pinned on their sides, but in this case the point of the pin should not be pushed right through the thorax, but should stop short at the side wall in order to avoid injuring the bristles in this region; as has already been noted they are of special importance in connection with the identification in the Muscidae. Cut off the head of the pin with a slanting cut, and pass the cut end into a piece of pith so that the uninjured side is uppermost. The legs and wings are then arranged with a needle, and supported in position with other pins until they are stiff.

Each specimen should then be mounted on a piece of cork or pith and this in turn mounted on a long firm pin; a label is attached giving the necessary details of time and place of capture. The labels should be as small as possible and of thin card or stiff paper, the supporting pin being passed through them. The pieces of cork are best prepared by covering a piece of cork mat neatly with paper, and then cutting it into small squares with a sharp knife; each piece should be a little bigger than the fly. Pith can be bought in sticks which can be shaved off into small strips.

For the examination of pinned specimens, and for use during the necessary manipulation, a lens magnifying about ten diameters should be used. The best form is one which fits into the eye like a monocle, leaving the hand free, but in the tropics it is essential to have a form which will permit of the free circulation of air between the glass and the skin, otherwise the glass will rapidly become dim owing to the deposition of a film of moisture, which obscures the vision and is most troublesome, necessitating constant wiping of the lens. This is best obtained by having a skeleton framework of aluminium to support the eye-piece.

Collecting Box

For storing diptera the method devised by Lefroy and Howlett is strongly recommended. The boxes used by the authors were made at a cigar factory, and are of cedar wood, not specially finished so as to be air-tight, but resembling the kind made to hold fifty long cigars, only a little longer. It is better to have a number of small boxes rather than a few cumbersome ones. The floor of the box is prepared as follows ; cork mat, preferably the prepared kind, is cut up so as to fit the floor of the box. A quantity of paraffin wax is then melted and to it is added napthaline in the proportion of one to four. A thin layer of this is then poured on to the floor of the box, and the cork pressed into it till it sets. More paraffin and napthaline mixture is then poured on to fill up all the crevices and to form a layer a quarter of an inch deep over the cork. The wax should be very hot when added and the box held flat till it has set. Any air bubbles which form may be removed with a hot knife. The boxes so prepared keep out all destructive insects, including ants. A plug of cotton wool on which is placed a few drops of essence of mustard is pinned in one of the corners ; this helps to keep the box free of moulds in the rainy season in the tropics. A small bag filled with crystals of carbolic acid should be pinned in another corner, for it also helps to prevent the growth of moulds. In moist climates it is useful to have a small tube containing some anhydrous calcium chloride firmly secured in another corner of the box ; when the calcium delequeses it should be renewed. The lid of the box may be fastened in position by a small clip or by an elastic band. The boxes are easily stored in a rack or small cabinet, the contents being indicated by a label on one side.

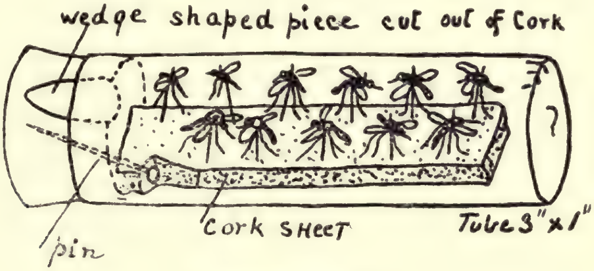
As a further precaution against injurious insects a few drops of the following fluid placed on some cotton wool in the corner of the box will be found useful.

Saturated solution of napthaline in chloroform . . . ten parts.
Creosote . . . . six parts.

This fluid should never be used in large quantities, nor should it be allowed to come in contact with the body of a fly ; it almost immediately turns it black.

In damp climates the following method for preserving delicate blood-sucking Diptera, such as mosquitoes, *Phlebotomus*, *Culicoides*, etc., is recommended. The fly is mounted on a card or cork disc in the usual way, and the pin supporting the cork is passed into the inner side of the cork of a small specimen tube instead of into the collecting box. A small wedge-shaped piece is cut out of the cork to allow of communication with the external air ; the whole tube with its contained specimen is placed in a dessicator. The tin box used for drying cigars, with a compartment at the bottom separated from the rest of the tin by wire gauze and containing anhydrous chloride of calcium, serves the purpose quite well. The tubes are placed in the dessicator for three or four days ;

the hole in the cork is then rapidly plugged with a pledget of wool and the cork sealed at once by dipping it in melted paraffin. In this way specimens can be kept in a dry condition in any climate. When it is desired to examine them the cork is removed, and when the specimens are replaced in the tube it is again placed in the desiccator for a few days and sealed as before. This is the method recommended by the Central Malarial Bureau at Kasauli for the preservation of mosquitoes. If it is desired to keep more than one specimen in the same tube, the flies should be pinned to a strip of thick cork, say two and a quarter by half an inch, one end of which is cut out in order to secure it to the cork of the tube with a pin. As before the cork of the tube has a wedge-shaped piece cut out so that the specimens may be dried and the tube sealed. Text figure 2, which is copied from a paper in *Paludism* by Major Christophers, I.M.S., shews this method of preserving mosquitoes.



TEXT FIGURE 2

For cutting out card discs it is convenient to have a gun wad punch, size No. 12 or No. 20. These discs are very useful for mounting mosquitoes which are to be put up in tubes. A very fine pin should be used, and passed through the thorax from the ventral side. The head of the pin is then cut off with a slanting cut, and the sharp end left is inserted in the disc, and held in place by a drop of sealing wax on the reverse side.

Preservation of early stages of Diptera; eggs

The preservation of the eggs of diptera in a condition suitable for study is a difficult matter. They do not make satisfactory or permanent preparations if mounted in glycerine, Farrant's solution or canada balsam. The problem appears to be solved, however, by Major Perry, I.M.S., who very kindly shewed the authors his method as applied to the eggs of mosquitoes. The eggs are placed in five per cent. formalin and drawn up from it into a glass tube, the calibre depending on the size of the eggs. The formalin is then allowed to flow out, and as it does so it leaves the eggs adhering to the sides of the tube, with a film of the solution. The ends of the tube are then sealed in the flame in the ordinary manner, so that the formalin cannot evaporate any further. For most purposes the eggs can be examined sufficiently well through the glass, but if a closer examination under a high power is required, they may be washed out of the tube with five per cent. formalin. If a fairly long piece of capillary tube is left at each end the same one can be used after it has been opened several times ; care should be taken to cut the tube with a file before attempting to break it.

Larvae and pupae

Larvae of diptera should be taken just before they become full grown, but while still feeding, as the shape is apt to alter the last day or so before pupation. They are best killed by dropping them into boiling seventy per cent alcohol, as this stretches them out. The alcohol is heated in a small evaporating basin or frying pan, thus minimizing the danger of it catching fire. The specimens should then be transferred to fresh seventy per cent alcohol, and preserved in small specimen tubes, the corks of which should be sealed with paraffin. The spirit should be renewed every three months and fresh corks inserted. A slip of paper with the details of the age, species, where taken, etc., written *in pencil* should be placed in the tube. Small larvae may be dehydrated, cleared in clove oil, and mounted in canada balsam. The cover slip may be supported, if necessary, with fragments of glass or with two pieces of fine capillary tubing, in order to prevent the cover slip from pressing on the specimen. Pupae can be preserved in the same way as larvae. The puparia of the Muscidae are best mounted on slips of card which may be pinned next to the imagines in the store box.

It is frequently necessary to make special preparations of particular parts of the fly for purposes of identification, as for instance the external genitalia of *Glossina* and *Phlebotomus* ; the wings of the latter, the heads of mosquitoe larvae, etc. The method of making cleared preparations is fully described in Chapter XI.

The isolated worker is often at a loss to know to whom to send his specimens of blood-sucking diptera for identification. The following addresses of well-known experts on each of the families and genera may be found useful.

Ceratopogoninae ... Professor J. J. Kieffer, Bitsch, Germany.
Simulium ... Professor Mario Bezzi, via Pio Quinto, No. 3,
Torino, Italy.

Phlebotomus ... Professor Newstead, F.R.S., School of Tropical Medicine, Liverpool. The Indian species should be sent to Dr. Annandale, Indian Museum, Calcutta.

Culicinae ... Mr. F. V. Theobald, Wye Court, Wye, Kent. Or the Central Malaria Bureau, Kasauli, Punjab, India.

Muscidae ... Professor Bezzi; Mr. Austen, British Museum (Natural History), South Kensington, London.

Tabanidae ... Miss Ricardo, British Museum (Natural History); Baron J. M. R. Surcouf, Museum National D'histoire Naturelle de Paris, France.

Pupipara ... Dr. P. Speiser, Kgl. Kreisartz, Labes, Pommern, Germany.

DISSECTION

The dissection[*] of dipterous insects does not usually present much difficulty, if the task is approached with some knowledge of the anatomy of the parts. Those usually required for examination, the alimentary tract, salivary glands, and ovaries, can be drawn out by traction, the mid-gut, hind-gut and ovaries through the posterior end of the abdomen, the anterior part of the alimentary tract and the salivary glands through the neck.

In all cases the wings and legs should be removed before commencing the dissection, and if possible the latter should be torn off at the junction with the thorax. The removal of the appendages may be carried out with the fingers or with fine scissors and forceps; in the case of small hairy or scaly insects the vestiture should be removed as far as possible by means of a soft brush. The debris of appendages and vestiture must on no account be allowed to fall on the slide on which the dissection is to be carried out, or it will cause trouble by adhering to the soft parts.

Small Nematocera

The following method will serve for the dissection of the posterior part of the alimentary canal and the reproductive organs from small Nematocera, such as *Phlebotomus*, *Simulium*, and the Culicidae. Place the trimmed insect on a slide with the posterior end of the abdomen towards you and just touching the

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[*] A general account of the technique of dissection, with description of the apparatus required, will be found in Chapter XI, which is intended as an introduction to the detailed methods described under each group.

edge of a small drop of saline. It is best to have the specimen on its back, but this is not essential, and it is sometimes difficult to retain it in this position, as in the case of hump-backed flies or those with a long bent proboscis. Place a pointed needle on the right edge of the penultimate segment, holding it with the left hand, but without making any attempt to cut. The pressure of the needle will push the contents of the abdomen to the opposite side, leaving a small piece of flattened integument in the region of the point. Now take a sharp lancet-shaped needle in the right hand, and cut the integument outwards from the point of the first needle, severing either the chitin or the inter-segmental membrane. Repeat the manoeuvre on the opposite side, thus freeing the terminal portion of the abdominal wall from the rest, or else so weakening it that it will tear easily, and then draw the insect further into the drop of saline. Unless the salivary glands of the same specimen are required, the head should be cut off at this stage with a sharp lancet-shaped needle; it should never be pulled off. This severs the attachment of the gut in front, so that its only connection with the thorax and abdomen is through small tracheae and lobules of fat body. Now place one needle on the thorax, holding it flat against the most posterior part, but without exercising any pressure, place the other on the last segment, and make a series of slow steady pulls towards you, holding the thorax steady at each pull. The alimentary tract and the reproductive system, which are attached at the hind end of the body but now free in front, will emerge from the abdominal segments. As the organs come out the lateral tracheae will show up as silvery white tubes on each side, and should be cut through to release the tension. After a few pulls the whole alimentary tract up to the oesophagus and the organs of reproduction will become free from the abdomen, and will retract. The oviduct, or the vasae, are now cut through, and any tracheae uniting the two systems severed by the needle. The two parts are separated, and the one which is required removed to a clean slide for examination.

Unless there is some special reason for doing so, the mid-gut should not be dissected until the contents have been at least partially digested. If one attempts to get it out while distended it may rupture, and in any case the pressure at the narrow end of the abdomen, through which it has to be drawn, will force the contents of the posterior part forwards, and thus possibly introduce a fallacy into subsequent observations. If it is necessary to dissect it while full of fluid blood one of the lateral walls of the abdomen should be cut up with a sharp needle to enlarge the aperture, and the process of drawing it out should be carried out very gradually, to allow the natural peristalsis of the muscular wall to thrust the contents down to their proper place.

If the ovaries are mature, and if they are not required for examination, some at least of the mature ova should be released through a slit in the wall, to make more room to work.

Dissection of the salivary glands

The salivary glands of the small Nematocera are a little difficult to dissect, as even with a dissecting microscope of moderate powers one cannot see them very clearly. They lie in the anterior and ventral part of the thorax, below the main mass of muscle, and are obtained by drawing them through the neck. The following method is that usually employed, and the one recommended for the examination of the glands of mosquitoes. Place the specimen, freed from its appendages and vestiture as before, on its side with the proboscis towards you. Steady the thorax with a needle held in the left hand, and place another needle, held in the right hand, behind the head. Then make a series of short and gentle pulls, drawing the head towards you and into the drop of saline. If this is done gently and carefully the integument of the neck and the muscle fibres attaching it to the thorax will rupture, while the duct of the salivary glands remains intact, and is pulled out of the neck and thorax with the glands still attached. The delicate oesophagus ruptures and retracts into the thorax; the pair of cervical tracheae (see page 68) often require to be cut with a needle. When the head is free it will be found that it has attached to it a small mass of whitish tissue, which consists of some fat body, muscle fibres, a part of the main nerve trunk, and the glands. The mass should be freed from the head by a sharp cut with a lancet-like needle, and moved gently in the saline. The glands can usually be easily differentiated from the other tissues by their glistening appearance, and may be isolated, though this is not usually necessary in routine examinations.

If the salivary glands and the alimentary tract are required from the same specimen, the salivary glands should be dissected out first. The oesophagus ruptures when the head is pulled away, and retracts into the thorax.

The Tabanidae

The dissection of the Larger Nematocera, such as the Tabanidae, is carried out in the same way. It is better, however, to use a paraffin trough rather than a slide, on account of the large size of the organs. The salivary glands of the Tabanidae extend into the anterior end of the abdomen, and cannot be extracted by the anterior route with the same certainty. If both glands are required intact the best procedure is to open the thorax down the middle dorsal line, and to evert the two halves, thus separating the muscle bundles between which the glands lie, and rupturing the small tracheae which hold them in position. The arch of chitin at the thoracic inlet is then broken through very cautiously, and the head pulled away from the thorax as in the dissection of the smaller flies. As soon as the expanded portion of the proventriculus comes into view, the oesophagus anterior to it is cut across, and the organ allowed to retract. The large cervical tracheae and the nerve cord are also cut, so that the only structure connecting the head with the thorax is the common duct of the salivary glands. When this has been isolated and seen, thrust a needle through the middle of the head and turn it so that the proboscis points forwards, thus keeping the duct in a straight line. After a few gentle tugs the glands emerge from the thorax.

When dealing with large insects, such as *T. albimedius* or *striatus*, especially when the mid-gut is full of blood, it is best to nip up a piece of the integument at one side with a pair of fine forceps, and then to slip one blade of a fine pair of scissors underneath, and to cut down as far as possible. When this has been done the dorsal wall can be reflected to the opposite side and cut off entire. In dealing with Tabanidae great care should be taken to prevent the duct of the crop becoming entangled with muscle fibres, if it or the proventriculus is required for examination.

Dissection of Muscid flies

The dissection of the Muscid flies is a little more difficult on account of the greater length of the alimentary canal and the extension of the salivary glands into the abdomen. The alimentary tract of female flies may be extracted by the following method. Having pulled off the legs and wings, grasp the fly by the head in the left hand, holding it firmly. This results in the extension of the ovipositor, owing to the displacement of air from the head to the hinder part of the body. As soon as the ovipositor is extended lay the fly, still grasped in the left hand, on a slide, with the ovipositor in a drop of saline; take a pair of fine forceps in the right hand, and pinch up the membrane at the base of the ovipositor, between the fifth and sixth segments. Make a steady pull, and the body wall will rupture at this point, the ovipositor, with the posterior attachment of the gut, being drawn out. It brings with it the whole of the internal organs, the alimentary tract rupturing at the junction between the oesophagus and the proventriculus. The coils of the gut are very complex, and great care should be taken to distinguish between the part in front of the Malpighian tubes and that behind.

The alimentary tract of male flies, and of females which have only a short ovipositor, is extracted by the same route, after incising the membrane between the last and the penultimate segment, as in the case of the Tabanidae.

It is not possible to extract the salivary glands of Muscids through the neck until their attachments, which consist of small but numerous tracheal twigs passing between the glands and the gut, have been severed. The following method is that usually employed. Hold the fly in the left hand, between the finger and thumb and with the dorsal surface uppermost. Take a sharp knife or a razor, and make a longitudinal incision in the middle line of the thorax and abdomen, carrying it as far down as possible, but making it just deep enough to pass through the chitin without injuring the soft structures. Then lay the fly in a drop of saline, and tear the two sides of the incision apart, completing it at the junction of the thorax and abdomen with a few cuts from a sharp needle. The coils of gut and gland come into view on the removal of the fat body, and there is usually no difficulty in separating them. The muscles of the thorax should be separated in the middle line, and the anterior and dorsal boundary of the neck broken through. The fly is now turned over on its side, and one needle thrust through the middle of the head. A cut is made with a sharp needle to sever the pharynx from its attachment to the head, and the needle then passed through the basal part of the proboscis (the bulb in the Stomoxydinae). The long glands can now be drawn out of the body while still attached to the hypopharynx.

Dissection of Hippobosca

The dissection of pupiparous flies, especially when in an advanced stage of gestation, is very tedious and difficult, owing mainly to the leathery nature of the integument and the very rich tracheal supply which goes to the uterus. The abdomen, in the case of *Hippobosca*, for instance, is best opened by cutting around the lateral borders with a pair of fine scissors, until the whole of the dorsal wall can be raised as a flap. The uterus should next be isolated by cutting through all its tracheae, and then removed by cutting across its lowest portion with scissors. It is not possible, or at least extremely difficult, to get out the alimentary tract until the uterus and its tracheae have been got rid of.

Dissection of larvae

The dissection of larvae is, as a rule, easy enough, the whole of the alimentary tract coming out by the posterior route; it is well to detach the last segment and make a few pulls to bring out the posterior part of the alimentary tract before cutting off the head to free the anterior attachment, as by doing so the gut is kept straight. If circumstances permit it is advisable to starve the larvae for a short time before dissecting them, in order to have the gut as empty as possible. In dealing with aquatic larvae, such as those of mosquitoes, this is done by keeping them in clear water.

Almost all the above dissections can be carried out without a dissecting microscope, especially after a little practice and some practical instruction, but a dissecting microscope renders the task so much easier that it is well worth the small cost and the trouble of transport. A watchmaker's eyeglass is very useful.

Important Literature on the Blood-sucking Diptera.

General

Brauer and von Bergenstamm.	Die Zweiflüger d. k. Museums zu Wien, 1880 to 1894. A somewhat rare work, dealing with the classification of Diptera.
Grunberg, K.	Die Blutsaugenden Diptera. Jena, 1907. A well-illustrated account of the tropical African flies.
Johannsen, O. A.	Aquatic Nematocerous Diptera in New York State, *New York State Museum. Bulletin* No. 68. Deals very fully with all the common forms, especially *Simulium*. The bibliography is fairly complete.
King, H. H.	Note on an Entomological Store-box suitable for use in the Tropics. *Bulletin of Entomological Research*, vol. iv, part I, 1913. The box mentioned in this note only differs from that described by the authors (page 415) in that the top and bottom is of three-ply wood, and the cork mat is held in position by glue; in Madras the authors have not experienced the difficulties met with by King in Khartoum.
Lefroy, H. Maxwell.	On the Collecting and Preserving of Insects. *Parasitology*, vol. iv, page 174, 1911.
Sharp, D.	Diptera, Chapter VII in *Cambridge Natural History. Insects*, Part 2, 1901. A good general account of the order, useful as an introduction to the study of the blood-sucking forms.
Schiner, J. R.	Fauna Austriaca. Die Fliegen Oesterreichs, 2 vols., 1862. A standard work on systematic dipterology; can still be obtained.
Williston, S. W.	Manual of the North American Diptera, third edition, 1908. Wm. Wesley & Son, 28 Essex Street, Strand, London. Deals with the external structure and classification of the diptera; all the families and the North American genera. An indispensable book.

NEMATOCERA

FAMILY CHIRONOMIDAE

AUSTEN, E. E.	Illustrations of British Blood-sucking Flies. *British Museum (Natural History)*, 1906. Contains illustrations of *Ceratopogon varius* and *C. pulicaris*.
Idem	Illustrations of African Blood-sucking Flies. *British Museum (Natural History)*, 1909. Contains drawings of three species of *Culicoides*.
Idem	Notes on African Blood-sucking Midges (Family Chironomidae, Subfamily Ceratopogoninae), with descriptions of new species. *Bulletin Entomological Research*, Vol. iii, part 1, 1912. Deals with *Culicoides grahami*, *C. brucei*, *C. milnei*, *C. distinctipennis*, *C. neavei*, *C. kingi*; *Johannseniella fulvithorax*; *Ceratopogon castaneus*, *C. incomptifeminibus* and *C. inornatipennis*.
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Idem	Etude sur les Chironomidae des Indes Orientales, avec description de quelques nouvelles espèces d'Egypt. *Memoirs of the Indian Museum*, Vol. ii, No. 4, 1910. Describes some Indian species of *Ceratopogon* and *Culicoides*.
LUTZ, A.	Beiträge zur Kentniss der blutsaugenden Ceratopogoninen Brasiliens. *Memorias do Instituto Oswaldo Cruz*. Tome iv, fasc. i, 1912. A general account of the structure and biology of early stages. Bionomics and breeding habits of imagines. Methods of collecting, preserving and studying the species.

See also Brunetti's recently published volume on Indian Nematocera in the *Fauna of British India*.

FAMILY SIMULIIDAE

Most of the older works dealing with the Simuliidae are inaccessible. Austen, in his *Illustrations of Blood-sucking Flies*, depicts several species. King, in the third *Report of the Wellcome Research Laboratories*, Khartoum, illustrates the larvae, pupae and imagines of *grisicollis* and *damnosum*. The following papers contain useful information on the biology of the Simuliidae :—

BARNARD, W. S.	Notes on the development of the Black Fly (*Simulium*), common in the rapids around Ithaca, N. Y. *American Entomologist*, Vol. iii, 1880. This paper contains a figure of the eggs.
BRUNETTI, E.	Indian Simuliidae in *New Oriental Nematocera*. *Records Indian Museum*, Vol. iv, No. 7, 1911.
LUTZ, A.	Beitrag zur Kentniss der brasilianischen Simuliumarten; *Memorias do Instituto Oswaldo Cruz*. Tome i, fasc. ii ; Zweiter beitrag zur Kentniss der brasilianischen Simuliumarten. *Ibid*, Tome ii, fasc. ii, 1909-10.

Osten Sacken, C. R. von. On the transformation of *Simulium*. *American Entomologist*, Vol. ii. Contains many references.

Riley, C. V. Report of Entomologist. *Annual Report. U. S. Comm. Agr.* for 1886. Gives a full account of life history and bionomics of *Simulium*.

FAMILY PSYCHODIDAE

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Howlett, F. M. Indian Sand Flies. *Transactions Indian Medical Congress*, section iii, 1909. The breeding places of *Phlebotomus*. *Proceedings of third meeting General Malarial Committee*, Madras, 1912. Govt. Press, Calcutta.

Lutz, H. and Neiva, A. Zur Kentniss der brasilianischen Phlebotomusarten. *Memorias do Instituto Oswaldo Cruz*, Tome iv, fasc. i, 1912.

Marett, P. J. Preliminary Report on the investigation into the breeding places of the sand fly in Malta. *Journal R. A. Medical Corps*, Vol. xv, No. 3, 1909. The life history of *Phlebotomus*. *Ibid.*, Vol. xvii, No. 1, 1911. Describes the method of breeding *Phlebotomus*.

Newstead, R. Notes on *Phlebotomus*, with descriptions of new species. Part 1. *Bulletin Entomological Research*, Vol. iii, part 4, 1912. See also Newstead, page 149.

FAMILY CULICIDAE

Annandale, N. A new genus of short-beaked Gnats from Ceylon. *Spolia Zeylanica*, Vol. vii, 1911. Describes *Ramcia inepta*.

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Cazeneuve, H. J. L'hivernation des moustiques dans la Chine du Nord. *Bulletin de la Soc. Path. Exot.* Tome iii, No. 3, 1910.

Christophers, S. R. Malaria in the Andamans. *Scientific Memoirs by Officers of the Med. and San. Depts. Govt. India*, new ser., No. 56, 1912.

Idem Contributions to the study of colour markings and other variable characters of *Anopheles* with special reference to the systematic and phylogenetic grouping of

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DARLING, S. T.	Studies in relation to malaria. Isthmian Canal Commission. ***Laboratory of the Board, Health Department of Sanitation***, Washington, 1910. A valuable paper on the *Anopheles* of the Canal Zone, Panama.
DÖNITZ, W.	Beiträge zur Kentniss der *Anopheles*. ***Zeit. für Hygiene***, Bands xli and xliii, 1902-3.
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Idem	On the classification of Mosquitoes. ***Canadian Entomologist***, Vol. xxxix.
EDWARDS, F. W.	Some new African species of *Anopheles* (sensu lato), with notes on nomenclature. ***Bulletin Entomological Research***, Vol. ii, part 2. The African species of *Culex* and allied genera (illustrated). ***Ibid.***, Vol. ii, part 3. A synopsis of the species of African Culicidae other than *Anopheles* (illustrated). ***Ibid.***, Vol. iii, part 1. A key for determining the African species of *Anopheles* (sensu lato) illustrated. ***Ibid.***, Vol. iii, part 3, Revised keys to the known larvae of African Culicinae (illustrated). ***Ibid.***, Vol. iii, part 4.
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BRACHYCERA

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CYCLORRHAPHA

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CHAPTER V

THE ORDER SIPHONAPTERA: FLEAS

THE Siphonaptera or fleas form a well defined group of insects, sharply differentiated from the other orders of insects by their structure and habits. Their origin is very obscure, but it is certain, from whatever form they may have originated, that they have no close connection with any other order of the present day fauna. In the past they have been classified as a sub-order of the Diptera, but there is little to support such an arrangement. They bear no recognizable traces of wings, and the structure of the thorax makes it very doubtful if they are descended from winged forms at all. From the simple type of segmentation, and the condition of the nervous system, they would appear to be comparatively primitive insects.

Fleas are laterally compressed in a characteristic manner, the only exception to the rule being found in the mature females of some of the Sarcopsyllidae. The mouth parts are formed for sucking and piercing, the order being exclusively blood-sucking and parasitic. They undergo a complete metamorphosis, the immature stages resembling those of Diptera. Each species is for the most part confined to one species of host, though to the general rule there are many exceptions, and it is found that in the absence of the elective host most species will feed on a variety of animals.

Relations to Disease —Natural Parasites

The chief interest of the order centres round their connection with plague, in the transmission of which from rat to rat and from rat to man fleas are the active agents. It is believed by some workers that the dog flea, and possibly the human flea, may play the part of invertebrate host in the transmission of the parasite of Kala Azar on the Mediterranean littoral.

Trypanosoma lewisi has been transmitted experimentally from rat to rat by two species of flea, *Ceratophyllus fasciatus* and *Ctenocephalus canis*. The early stages of tape worms have frequently been found in the intestines of fleas from the cat and the dog. A considerable number of protozoa have been recorded from the alimentary tract of adult and larval fleas, including at least four species of the genus *Herpetomonas* and two of *Crithidia*. Nöller found as many as twelve per cent of the dog fleas (*Ctenocephalus canis*) caught in November and December in Berlin infected with *Herpetomonas ctenocephali*, Fantham, this species having been previously noted by Fantham in England and Marzocchi in Turin. Three per cent of *Ctenocephalus felis* are infected with a similar parasite in Madras. *Herpetomonas ctenopthalmi*, Mackinnon, is found in *Ctenopthalmus agyrtes*, the common flea of field mice in England; *Herpetomonas pattoni*, Swingle, is recorded from *P. brasiliensis* * and *P. sp.*, from *Ceratophyllus lucifer*, Rothsch., and from *Ceratophyllus fasciatus* in France; *Ceratophyllus alladinis*, from the Indian squirrel, *Funambulus palmarum*, also harbours a *Herpetomonas*. *Xenopsylla cleopatrae*, which occurs on the jerboa in Egypt, is infected with a flagellate (*Herpetomonas?*). In *C. agyrtes*, in addition to the *Herpetomonas*, there is also a *Crithidia*, described by Patton and Strickland; *Hystrichopsylla talpae*, the mole flea, harbours *Crithidia hystrichopsyllae*, Mackinnon. Most important of all, *Pulex irritans* has been shown by Porter, working in England, to be naturally infected with *Crithidia pulicis*. The importance of the flagellates from fleas which are found on the dog and on man cannot be over-estimated, for they are, at one stage of their life history, practically indistinguishable from the parasite of Kala Azar. The early stages of the species occurring in *Ctenocephalus felis* and *Ceratophyllus alladinis* are passed in the Malpighian tubes of the larva, and are almost motionless; as the larva pupates the parasites mature and pass down to the hind-gut, where they may be found in the adult, forming a palisade around the wall. They are passed out in large numbers with the faeces of the flea. Probably all these flagellates reach the adult through the larva, and return to the larva when it absorbs the blood-containing faeces of the adult.

Gregarines are frequently found in the intestinal tract of adult and larval fleas. One is recorded by Ross in *Ctenocephalus 'serraticeps'*, from dogs in Egypt, and another by Strickland from *Ceratophyllus fasciatus*. Ashworth and Rettie have recently described a new species, *Stenina rotundata*, from several species of the genus *Ceratophyllus*; it was found most frequently in *Ceratophyllus styx* from the nest of the sand marten.

Malpighella refringens, Minchin, occurs in the rat flea, *Ceratophyllus fasciatus*, and was also found by Nöller in the dog flea. The dog flea also harbours a species of *Nosema* (Nöller). A spirochaete has been found in the larva of *Ctenocephalus felis* (Patton).

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* *cheopis*

EXTERNAL ANATOMY

The classification of the Siphonaptera is based upon such minute anatomical points, and the differentiation of species has been carried to such a pitch within recent years, that a detailed knowledge of the external characters of the group has become essential. The tedium of mere anatomical nomenclature is enlivened, thanks to the labours of Jordan and Rothschild, by many interesting points bearing on the relations between the structure of the flea and its environment, and on the phylogeny of the group.

The body in the Siphonaptera is compressed strongly in the lateral direction, with the evident advantage to the insect of enabling it to work its way the more easily among the hair or feathers of its host. Bugs and lice are compressed dorso-ventrally with a similar result. Compression is limited mainly to the thorax and abdomen, and is retained in the latter even when the ova are ripe, except in some Sarcopsyllidae. The segments are distinct from one another except in the head, and are arranged in a simple manner, one tergite and one sternite to each segment as a rule. There are ten segments in the abdomen, of which the terminal three are modified for sexual purposes. The wings, if ever they existed in ancestral forms, have left no trace.

The cat flea, *Ctenocephalus felis*, or the dog flea, *C. canis*, will serve as an example for descriptive purposes (Plate LIII). The former can be obtained from almost any kitten. It belongs to the Pulicidae, the central family of the Siphonaptera. The differences between the two species are very slight; they will be referred to later.

The head

The head is only slightly flattened laterally, its outline on section being that of an arch, high in the posterior portion. When seen from the side its outline is roughly triangular; the dorsal border is gently rounded from the dorsal and posterior angle to the distal ventral one. The posterior border, which is mainly vertical, though with a small tubercle projecting backwards in its upper part, articulates with the prothorax without the intervention of a neck. The ventral border is straight, and is armed with a row of stout and heavily pigmented spines, projecting well beyond the margin, and directed downwards and backwards. These spines (g. c., fig. 1.) constitute the *genal comb*; they are often referred to as *ctenidia*. The lateral area of the head on each side is divided into two portions, known as the *frons* and the *occiput* respectively, by the *antennal groove* (a. g.), which runs from the middle of the ventral border upwards and forwards.

PLATE. LIII.

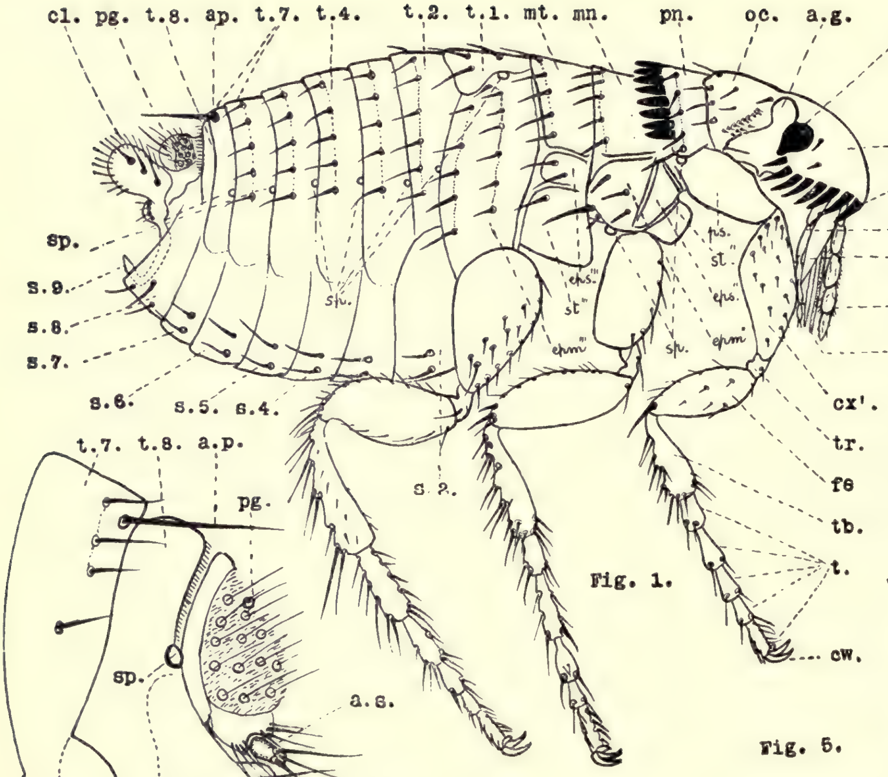
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Fig. 1.

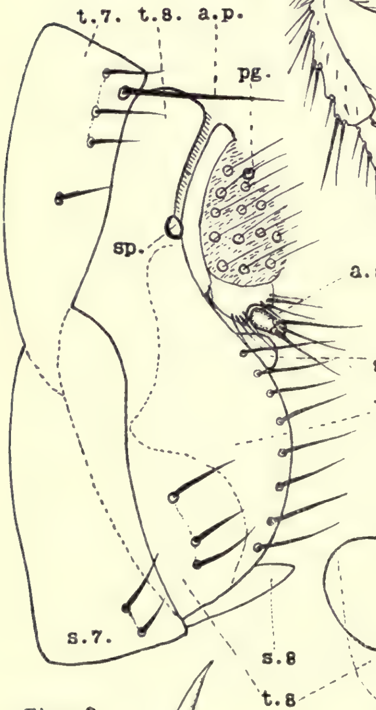
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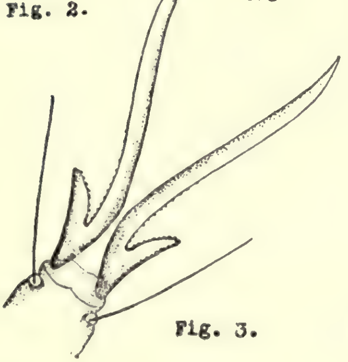
Fig. 2.



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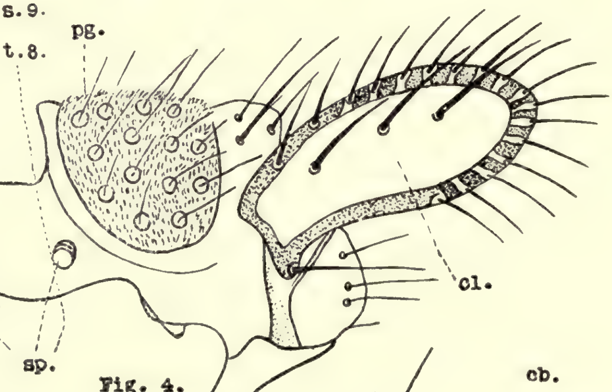

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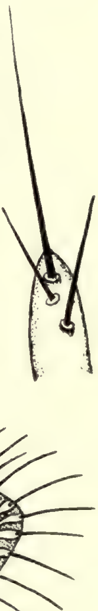


Fig. 5.

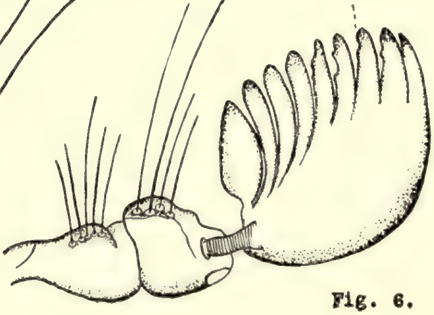


Fig. 6.

PLATE LIII

Figure 1.	*Ctenocephalus felis*, ♂. To illustrate the external anatomy. The manubrium of the clasper is overlapped by the ninth sternite. × 40.
Figure 2.	The terminal segments of *Ctenocephalus felis*, ♀. The dotted line on the eighth tergite indicates the extent of the ninth sternite, which lies below it. × 110.
Figure 3.	The claw as seen when flattened out. Note the serrations and the chitinous pad at the base.
Figure 4.	The ninth tergite of the ♂ of same, showing the manubrium, and pygidium. × 240.
Figure 5.	The anal stylet of the ♀ of same. × 300.
Figure 6.	The antenna. It is segmented only on the posterior surface.

REFERENCE LETTERS, PLATES LIII TO LVIII.

a.g.	Antennal groove.	mn.	Mesonotum.
ant.	Antenna.	mp.t.	Malpighian tubes.
ap.	Antipygidial bristle.	mt.	Metanotum.
c.d.	Common salivary duct.	mx.	Maxilla.
cb.	Club of antenna.	mx.p.	Maxillary palp.
ch.	Chitin of head capsule.	oc.	Occiput.
cl.	Clasper.	oes.	Oesophagus.
cw.	Claw.	p.	Penis.
cx.	Coxa.	p1-3.	Processes of the clasper.
d.w.	Dorsal wall of pharynx.	pg.	Pygidium.
e.	Eye.	ph.	Pharynx.
e.d.	Ejaculatory duct.	pn.	Pronotum.
ep.	Epipharynx.	pv.	Proventriculus.
epm.	Epimerum.	r.s.	Receptaculum seminis.
eps.	Episternum.	rt.	Rectum.
f.t.	Fibrous tissue.	s.2—s.10.	Sternites in order.
g.c.	Genal comb.	s.c.	Spine of the genal comb.
g.h.	Genal hook.	s.h.	Sense hair.
hy.	Hypopharynx.	sl.d.	Salivary duct.
h.g.	Hind-gut.	sl.g.	Salivary groove.
i.c.	' Internal incrassation '.	sp.	Spiracle.
l.ep.	Labrum-epipharynx.	st.	Sternum.
l.p.	Labial palp.	t.	Tarsus.
lb.	Labrum.	t.1.—t.9.	Tergites in order.
m.	Manubrium.	tb.	Tibia.
m.g.	Mid-gut.	td.	Tendon.
mb.	Membrane.	tr.	Trochanter.
md.	Mandible.	v.w.	Ventral wall of the pharynx.

The marks ″ and ‴ signify that the parts belong to the second and third segments of the thorax respectively.

The groove in the cat flea is open at the lower end, but in many forms it becomes closed by the extension backwards of the ventral border of the frons. (Plate LVI, fig. 5.) It is closed at the upper end, so that the grooves of the two sides are not continuous with one another. The amount of upward extension of the groove varies in the different genera. In some cases it extends only a short distance upwards, and is continued towards the dorsal border by an internal thickening or 'incrassation', (Plate LIV, fig. 1) believed to be due to the coalescence of the two sides of the groove at its upper end. The eye is situated anterior to the middle of the groove. It is non-facetted, and is conspicuous on account of its dense pigmentation. In many fleas the eye is absent or vestigial (Plate LVI, figs. 2 and 5).

Antennae

The *antenna* lies deeply in the antennal groove, and is thus protected from injury when the insect moves about among the hairs, exactly as is the case in the Pupipara, which have a similar habit. It consists of three joints (Plate LIII, fig. 6), of which the distal one, known as the 'club', is much the largest, and is specially modified. The club is a large oval body, divided along its posterior border into a number of pseudo-joints, the intersections between which do not extend far into the substance of the organ. The amount of segmentation in the distal joint of the antenna differs in different genera, and is a point of taxonomic importance. In many forms, as for instance *Ceratophyllus* (Plate LIV, fig. 12), the antenna is distinctly segmented all the way round, instead of only on the posterior border. The middle joint of the antenna is short and ring-like, and bears four delicate and faintly pigmented hairs of considerable length, but extremely fine, and generally only recognizable when the antenna is dissected out of its pit. The proximal joint is narrow but longer, and bears a row of five hairs, shorter than those of the middle segment, but of equal tenuity.

The indentation of the wall of the head capsule by the antennary grooves on the two sides divides the head cavity into two portions, the upper one of which contains the pharynx.

The mouth parts of the flea are adapted for sucking and piercing, like those of the Diptera, and though the differences between the two types are considerable, the homology can be followed closely enough to be of service in explaining the anatomy and mechanism.

The parts present are the same as those in the Nematocera, the least specialized Diptera, namely, *labrum* and *epipharynx*, fused to form a compound organ, and the *hypopharynx;* the *mandibles*, *first maxillae*, and the *second maxillae*, these latter being only partly fused together, yet fulfilling the same function of forming a sheath for the piercing parts. The essential difference between the conditions in the Siphonaptera and those in the Diptera is that in the former the hypopharynx has failed to develop in the same degree, and does not extend beyond the base of the proboscis. It can consequently take no part in the formation of the food canal, nor can it convey the saliva into the wound. Its place in both these functions is taken by the mandibles, which, by apposition with one another and with the epipharynx, form a channel for the conveyance of the food, and which have grooves on their inner sides to conduct the saliva downwards from the salivary receptacle to the wound. There are thus, as in the Diptera, two canals, one afferent and one efferent.

The Mouth Parts

The mouth parts project downwards, and, in the Pulicidae, usually a little backwards, from the distal portion of the ventral surface of the head; their proximal ends, in the cat flea and its allies, are concealed by the genal comb. The aperture through which they emerge from the wall of the head cavity is surrounded by thinner chitin, and may be termed the *peri-oral ring*. There is no membraneous area such as is found in this situation in the Diptera. When seen in cleared and mounted preparations the parts are usually a little displaced from their natural positions. The maxillary palps lie in front, and are the most conspicuous parts of the apparatus, projecting from the front of the head like antennae; the maxillae are frequently displaced from the labium, which normally ensheaths them, and lie in front of it.

The labrum-epipharynx

The *labrum-epipharynx* (Plate LIV, figs. 11 and 9), which has been described as the labrum and also as the epipharynx, is a long and slender organ, presenting a rounded contour on section, but flattened on its ventral surface where it is in apposition with the mandibles. Its dorsal wall, corresponding to the labrum, and its ventral wall, corresponding to the epipharynx, are composed of rigid yellow chitin, while the lateral walls which connect these parts are more membraneous. Within these walls there is a space (Plate LVIII, fig. 10) continuous with the haematocoele of the head, and limited distally by the fusion of the two parts, as in the Diptera. The labrum extends to the distal extremity, the two parts taking about an equal share in the formation of the compound organ. The lateral edge of the labrum bears fourteen pairs of forwardly directed tubercles of extremely small size. They are not cutting teeth, but are probably sensory organs, as under a high magnification a central canal can be distinguished in them. Proximally the chitinous portion of the labrum ceases at the peri-oral ring, to the margin of which it is attached by a narrow band of membraneous chitin. The epipharynx, or ventral lamina of the compound organ, has no attachment to the wall of the head cavity, but is continued inwards in direct chitinous continuity with the dorsal wall of the pumping organ, as in the Diptera. The distal end of the labrum-epipharynx is blunt and rounded, and is not provided with teeth or tubercles.

The *hypopharynx* (Plate LIV, fig. 11) is rudimentary, and can only be seen in dissections, and even then it is by no means easy to find. It consists of a small but thick triangular plate, continuous behind with the salivary receptacle, and projecting forwards between the epipharynx and the mandibles at the base of the proboscis. It is pierced through its centre by the salivary duct, which opens at its pointed apex, permitting the saliva to flow into the grooves of the mandibles immediately distal to it.

The mandibles

The *mandibles* (Plate LIV, figs. 7 and 8) are the most important parts of the mouth apparatus, as they are the only cutting weapons; they also take part in the formation of the food canal, and convey the saliva to the wound. In their method of action and articulation they correspond more closely to the first maxillae in the Diptera. Each mandible is a broad blade, rounded in contour at the proximal end, but flattened for the most part of its length, the surfaces of the two blades being inclined backwards and inwards from the externa border. At the proximal end the internal surfaces are in contact with the hypopharynx, but where this short piece ceases they come to lie in contact with the epipharynx, forming the lateral sides of the food canal; from this point the flattened blades are inclined more vertically. On the inner side of each mandible there is a groove, commencing at the point where the hypopharynx ceases, and narrowing as it proceeds distally, until in the distal half of the blade it is almost closed by the approximation of its edges. The grooves receive the saliva from the canal in the hypopharynx, and convey it to the distal end of the proboscis (Plate LVIII, fig. 9).

The distal two-thirds of the external surface of the mandible is beset with minute hook-like teeth (Plate LIV, fig. 7), arranged in three or four rows, and directed towards the base of the blade. They are not set on the extreme edge, as this is very much attenuated and soft, so much so that it is difficult to define under the microscope. The purpose of this membraneous expansion is of course to ensure that the canal formed by the mandibles and epipharynx shall be closed tightly during the act of sucking.

The mandible is provided with a second joint (Plate LIV, fig. 8) at its proximal end, by means of which it is articulated to the wall of the head capsule in very much the same way as that in which the maxilla of *Tabanus* is attached. This joint consists of a stout rounded rod of chitin, attached to the base of the blade by its expanded distal end. Its proximal end has on it a stout tubercle, separated from the rod by a short neck, which is fitted into a small pit of corresponding size and shape in the genal border of the head, immediately internal to one of the spines of the comb. The rod is thinner beyond the tubercle, and terminates in a blunt point. The exact disposition of the muscles acting on the joint has not been ascertained ; there is one well-defined bundle, terminating in a short tendon, which is inserted into the expanded distal end of the rod. Other short muscles appear to pass between the proximal end of the rod and the wall of the head, while other fibres are attached to the pointed internal end proximal to the tubercle.

The method of action of the mandible is evidently very similar to that of the maxilla of *Tabanus*. The internal rod, which corresponds to the cardo, rotates on the articulation between the tubercle and the pit in which it lies, the two forming a simple cup and ball joint. The excursion will be at least through a right angle, and as the distal end passes forwards it carries with it the blade, which is thus protracted through the wound.

The first maxillae

The *first maxillae* (Plate LIV, fig. 4) of the flea are not cutting organs, and probably do not enter the wound. They lie in a plane anterior but external to that of the mandibles. Each consists of two portions, the palp and the blade, the latter being often referred to as the ' flap '. The blade is a stout conical piece of chitin, apparently four-sided like a pyramid, and terminating in a stout elongated point. The palp is articulated to the base of the blade on its anterior and outer side, and hangs down in front of the other parts like an antenna. It consists of four joints of the ordinary type, of which the second is the longest, the first and fourth of about equal size, and the third the smallest. Each joint has a whorl of four hairs at its distal border, the second having in addition two whorls of four each in its middle, and the third one whorl. The hairs at the distal end of the palp are very small.

The *labium* (Plate LIV, fig. 6) is the most posterior of the mouth parts, and consists of two lateral portions, usually termed the labial palps, united

PLATE LIV

Figure 1. The head of *Echidnophaga gallinaceus.* × 130.

Figure 2. The hind coxa of *Pulex irritans*, to show the spines on the inner side.

Figure 3. The end of the manubrium of *Ctenocephalus canis.* Compare with that of *Ctenocephalus felis* on the previous plate.

Figure 4. The maxilla of *Ctenocephalus felis.*

Figure 5. The head of *Ctenocephalus felis*, ♀, after Rothschild. Compare with figure 13 below.

Figure 6. The labium (rostrum) of *Ctenocephalus felis.* The large undivided plate corresponds to the mentum, the smaller one posterior to it to the submentum. × 220.

Figure 7. The distal end of the mandible of *Ct. felis*, to show the teeth. Very highly magnified.

Figure 8. The mandible of *Ct. felis*, showing the basal segment and its articulation to the wall of the head cavity in the region of the genal comb. A part of the wall with one spine is shown, broken off. × 190.

Figure 9. The distal end of the labrum-epipharynx of *Ct. felis.* × 1000.

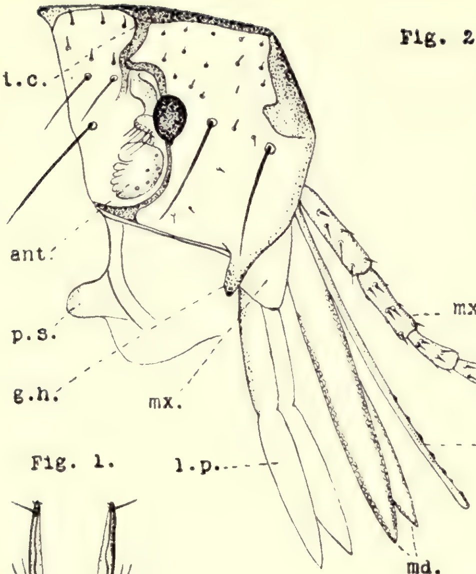
Figure 10. One of the sense hairs of the antenna of *Ceratophyllus fasciatus*, very highly magnified. See figure 12, where they are darkly shaded.

Figure 11. The labrum-epipharynx of *Ct. felis*, dissected out with its attachments. The salivary receptacle is situated in v. w. × 190.

Figure 12. The antenna of *Ceratophyllus fasciatus.* It is completely segmented. Compare that of *Ct. felis* on previous plate.

Figure 13. The head of *Ctenocephalus canis*, ♀, after Rothschild. Compare with figure 5 above.

PLATE LIV.


i.c.
ant.
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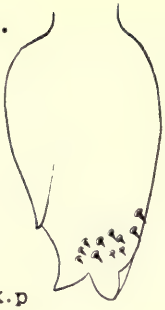
md.

Fig. 1.

Fig. 2.



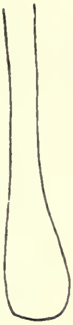
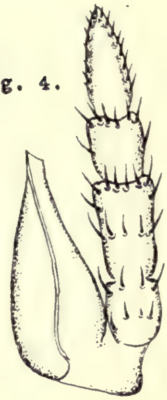


Fig. 3.

Fig. 4.



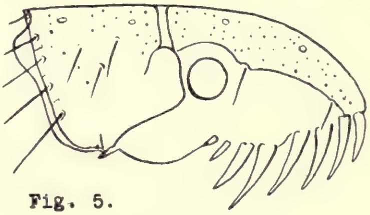


Fig. 5.

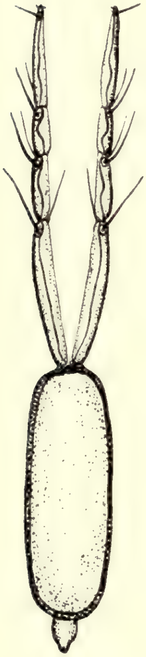


Fig. 6.

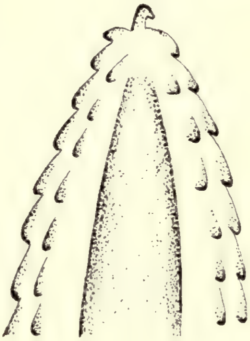


Fig. 7.

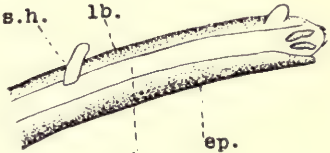


Fig. 9.

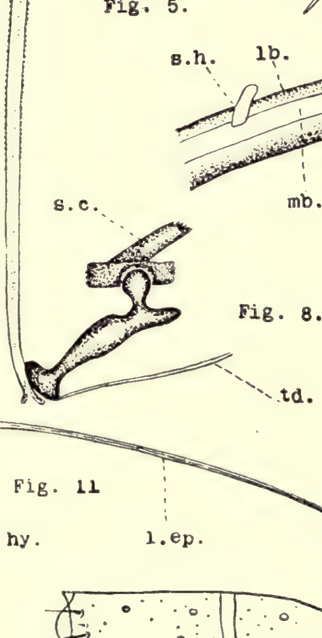


Fig. 8.

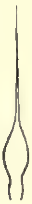


Fig. 10.

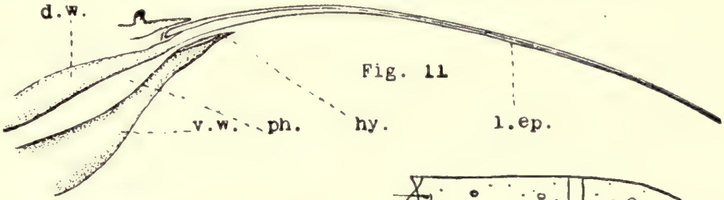
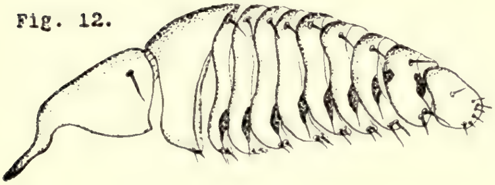

d.w.
v.w.
ph.
hy.
l.ep.

Fig. 11

Fig. 12.



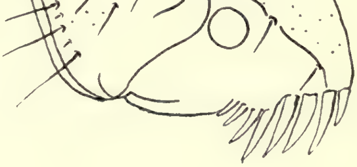


Fig. 13.

basally to a median piece. The whole is often termed the *rostrum*; the number of joints of which it consists is a point of importance in classification. The nomenclature is a little confusing, for it is by no means certain that the bilateral portions are really palps in the ordinary sense. The term rostrum, moreover, is used in connection with the Muscid flies to indicate the part of the head which is protruded to become a part of the proboscis. Its literal meaning renders it hardly applicable in the case of the flea.

The labium

The paired portions of the labium are slender jointed organs, each consisting of four segments. Of these the proximal one is the longest, being equal to half the length of the whole; the distal one is a little longer than the second and third. All the joints are flattened laterally and strongly concave on their internal surfaces, the two palps forming a sheath in which the mandibles and labrum-epipharynx are concealed in the natural resting condition of the parts. The outer surface bears a pair of hairs at the distal end of each joint. The distal end of the fourth segment is obliquely truncated.

The proximal portion of the labium consists of an oblong plate of thin chitin, to the distal end of which the paired portions are articulated. The plate is concave on its upper or dorsal surface, and extends from about the level of the middle of the maxillary flap to the peri-oral ring, and is thus concealed for a considerable portion of its extent by the genal comb. At its proximal end there is a smaller plate of chitin in the middle line.

The nomenclature of the parts which would bring the flea into line with other insects would be to regard the large basal plate as the mentum, and that proximal to it, and only visible in dissections, as the submentum. The paired portions may then be termed the labella, in which, in the case of the flea, four joints can be recognized. The whole labium is to be regarded as originally paired, and formed of the appendages of the sixth segment of the head, though there is little to indicate how much is appendage proper and how much is part of the head wall. It is hardly correct to speak of the labium as 'bifid'.

The mechanism of the mouth parts will be readily understood from what has been said with regard to that of the dipterous mouth. The wound is made by the protraction and retraction of the mandibles, retraction being the more effective movement of the two, as is shown by the direction of the teeth. The labrum-epipharynx cannot act as a 'pricker', as it has been termed, for it is blunt at the tip and has no cutting teeth.

Mechanism of the mouth parts

The maxillae, on account of their size and position, can only enter the superficial part of the wound if they enter it at all, and are not provided with a musculature which would enable them to assist in the cutting operation; possibly they assist in fixing the flea in position while the blood is being sucked up. The labial palps, or labella, do not enter the wound, but are bent to right and left as the mandibles enter the skin. Whether the bending of these organs is entirely a passive process, or whether there are intrinsic muscles to bring about the action as in the Diptera, it is impossible to say. It is noted by Jordan and Rothschild that they are less chitinized in the Sarcopsyllidae, which fix themselves to the skin of the host after the manner of ticks, than in fleas of ordinary habit.

The thorax (Plate LIII, fig. 1)

The three segments which compose the *thorax* are quite distinct from one another, and the joints between them permit of a certain amount of movement. The head is attached to the thorax without the intervention of a neck, but the joint between it and the prothorax is more freely moveable than are the others. Each segment consists of two plates, a tergite and a sternite, the former being undivided and simple, while the latter is fused more or less closely with certain sclerites representing the pleural plates as described in the Diptera.

The tergites are simple broad arched plates, extending over the dorsum and the dorsal half of the lateral aspect of the thorax. The pronotum bears on its hind edge a row of stout spines forming a comb like that on the genal edge of the head. This ***pronotal comb*** is absent in many fleas (Plate LVI, figs. 3 and 6). Both this and the genal comb are of service to the insect in facilitating forward progression among the hairs of the host.

The ventral plate of the prothorax is large and undivided, and extends as far forward as the level of the posterior margin of the eye, being only separated from the posterior portion of the genal edge by a narrow interval. In this and many other species it bears no hairs. The two prosternites are continuous with one another in the middle line of the ventral surface, where the chitin is thinner than elsewhere. The ventral plate of the mesothorax is divided by ridges into portions which have been homologized by Jordan and Rothschild with the ***sternum***, ***episternum***, and ***epimerum***; these ridges mark the lines along which the discrete plates were separated in a more primitive condition. It is divided into two approximately equal portions by a ridge running from the insertion of the coxa of the middle leg upwards and a little forwards, the upper extremity of the ridge being situated just posterior to the lower and anterior angle of the mesonotum. The portion behind this ridge is regarded as the epimerum; that in front of it is again divided into two parts by a second ridge arising in common with the first, but passing more obliquely forwards. The middle portion thus cut off, triangular in shape in this species, is the episternum, while the lobe in front of the suture, which is free on all sides except the posterior, is the sternum. The latter forms a conspicuous projection between the first and second pair of legs.

The ventro-lateral plate of the metathorax is of considerably greater extent, and passes backwards over the side wall of the abdomen for a considerable distance below the first abdominal tergite. It is divided into two by a vertical ridge, commencing at the level of the insertion of the coxa of the hind leg and continuous with the line of separation between the metanotum and the first abdominal tergite. The part anterior to the ridge is again divided into two portions by a horizontal ridge, the upper portion being the *episternum*, and the lower, which is much the larger, and which is continuous with its fellow of the other side by a softer portion of chitin, the *sternum*. The portion posterior to the vertical suture is the *epimerum*; it extends behind the metanotum and below the first abdominal tergite, and is the largest plate in the lateral wall. The epimerum is situated at the widest part of the body of the flea, and forms the base of the abdomen. The great development of this plate is, according to Jordan and Rothschild, a special feature of the Siphonaptera. It replaces the first abdominal sternite.

The abdomen (Plate LIII, fig. 1)

In the *abdomen* the sclerites are more regularly arranged than in the thorax. There are ten pairs in all, and of these the last three are specially modified for sexual purposes. The first abdominal tergite is broadest in the antero-posterior direction; it extends downwards on the lateral wall for only a short distance, and overlaps the epimerum of the metathorax. The sternite of the first abdominal segment is wanting. The plates of the second to the seventh segments are simple arched bands, diminishing in extent from before backwards in accordance with the shape of the body. The second sternite lies behind the epimerum and is overlapped by it. The dorsal plates are longer than the ventral ones, which they overlap. The eighth tergite and sternite are smaller than the rest, and the tergite is frequently telescoped inside the one in front of it, and is consequently only seen when the parts are dissected out. It becomes visible when the abdomen of the flea is distended.

External genitalia

The remaining segments differ in the two sexes. They are of the greatest importance from the point of view of classification and identification of species, as they present great variety of form, and provide reliable taxonomic characters. The parts can only be examined satisfactorily by dissection, after preliminary maceration in potash ; specimens should be mounted both in profile and flattened out, and in the case of the female in such a way as to permit of examination from the posterior aspect.

The most important of the terminal segments in the male is the ninth, which is of a most complex description ; part of it is visible externally, and part concealed beneath the segments anterior to it. At the posterior end of the abdomen, projecting upwards and backwards in a conspicuous manner, there is a pair of large oval plates (Plate LIII, fig. 4), each of which has a fringe of stout hairs around its periphery, and three or four longer bristles on its external surface ; these are the *claspers*, a part of the male accessory genital organs. Anterior to them, and occupying the greater part of the dorsal portion of the segment, there is on each side an oval plate termed the *pygidium*. The surface of this has on it a number of small clear areas, from each of which there projects a long and extremely fine hair. The space between and surrounding the clear spaces is beset with a dense coat of fine recumbent hairs, which are heavily pigmented, rendering the whole pygidium a prominent object in cleared preparations. The pygidium is evidently a sensory structure ; it occurs in all fleas, but its precise function is unknown.

The dorso-lateral portion of the ninth tergite extends a little distance posterior to the base of the clasper, and forms the distal extremity of the abdomen in the upper part. Anteriorly a projecting flange passes from its border underneath the eighth tergite. The ventral border of this flange and the posterior border of the sclerite converge at the posterior and ventral angle, and are here produced downwards and forwards into a conspicuous rod (m. in Plate LIII, fig. 4), which lies underneath the eighth segment, extending as far forward as does the flange. This is the *manubrium*, and to it are attached the muscles actuating the claspers.

The form of the ninth segment in the male *Ctenocephalus felis* is not very typical of the Pulicidae. The clasper is usually divided into several portions, as in *Pulex irritans* (Plate LV, fig. 6). The clasper is frequently spoken of as the ‘ moveable finger ’.

The tenth tergite is entirely internal, and is probably mainly absorbed into the complex penis sheath.

The ninth sternite has a characteristic shape. It consists of two

PLATE.LV

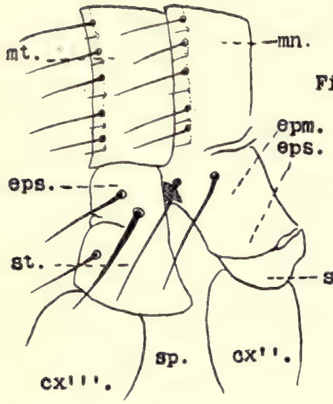

mt.
mn.
epm.
eps.
eps.
st.
st.
sp.
cx'''.
cx''.

Fig. 1.

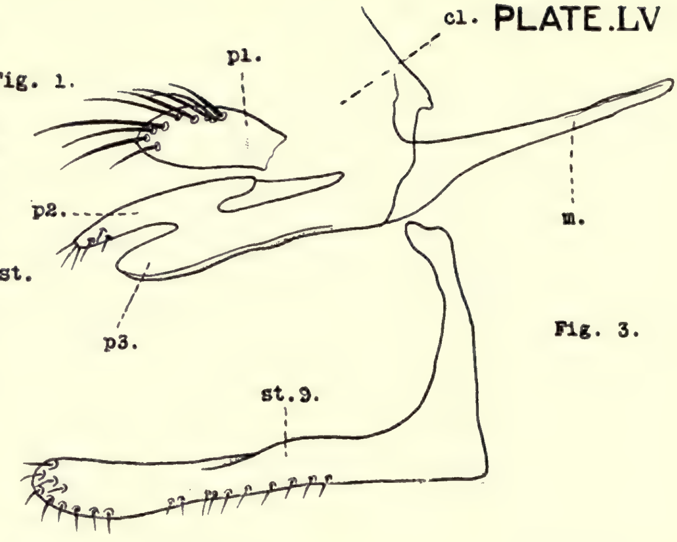

cl.
p1.
p2.
p3.
m.
st.9.

Fig. 3.

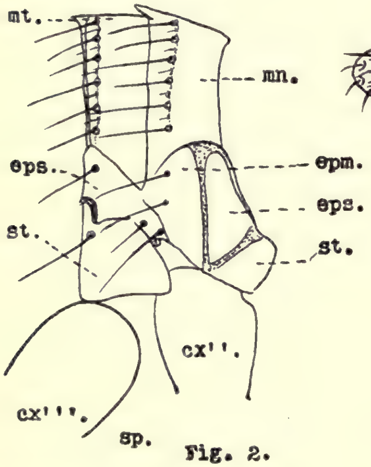

mt.
mn.
eps.
epm.
eps.
st.
st.
cx''.
cx'''.
sp.

Fig. 2.

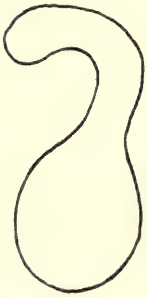


Fig. 4.

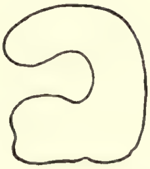


Fig. 5.

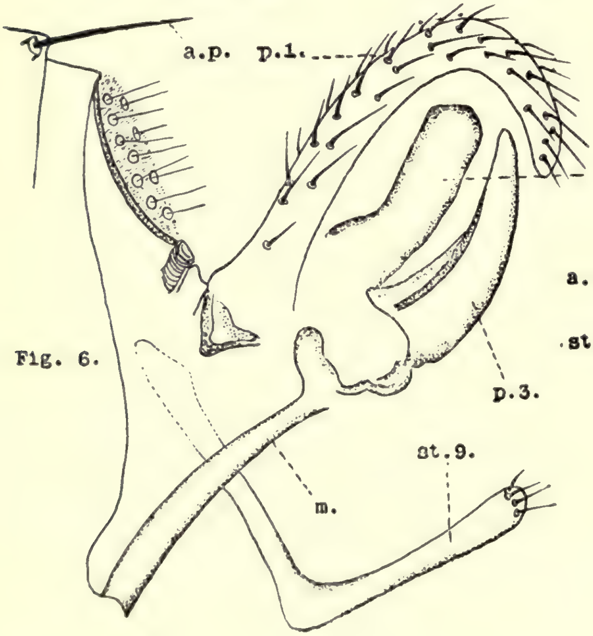

a.p.
p.1.
p.2.
p.3.
st.9.
m.

Fig. 6.

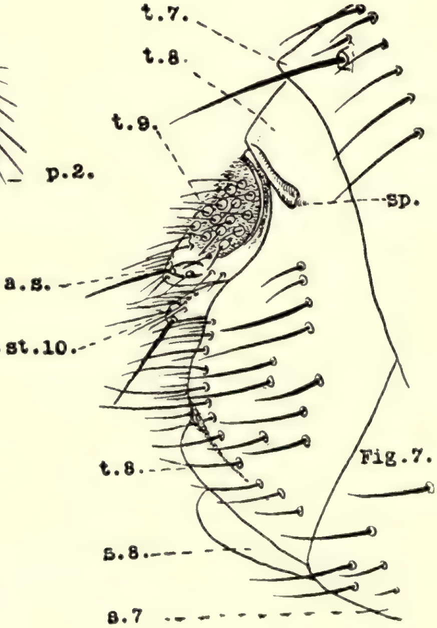

t.7.
t.8.
t.9.
sp.
a.s.
st.10.
t.8.
s.8.
s.7

Fig.7.

PLATE LV

Figure 1.	The meso- and meta-thorax of *Pulex irritans*. ×66.
Figure 2.	The same of *Xenopsylla cheopis*. ×66.
Figure 3.	The ninth tergite and sternite of *Xenopsylla cheopis*, ♂, after Jordan and Rothschild.
Figure 4.	The spermatheca of *Pulex irritans*. ×125.
Figure 5.	The same of *Xenopsylla cheopis*. ×125.
Figure 6.	The terminal segments of *Pulex irritans*, dissected out, ♂. ×120.
Figure 7.	The terminal segments of *Xenopsylla cheopis*, ♀, after Jordan and Rothschild.

parts, one vertical and the other horizontal, united together to form the 'boomerang rod' (cp. Plate LV, figs. 3 and 6). The vertical portion is internal, and is concealed by the eighth sternite, while the horizontal part, also mainly concealed, projects distally from the end of the abdomen, and bears a few hairs. In many preparations, and in the one from which figure 1, Plate LIII, was made, the vertical portion of the boomerang rod and the manubrium of the ninth tergite lie in the same plane, and cannot be readily distinguished from one another.

Terminal segments of female

The terminal segments in the female (Plate LIII, fig. 2) are somewhat compressed. The eighth tergite is narrow in the dorsal line, but expands laterally and extends almost to the ventral line, thus occupying almost the whole of the lateral area of the terminal part of the abdomen. The eighth sternite is correspondingly reduced, and forms an inconspicuous plate below the tergite. The ninth tergite bears the pygidium as in the male, and is comparatively small. Immediately below it there is a small conical projection, bearing a tuft of hairs, known as the *stylet* (Plate LIII, fig. 5); this and the small plate posterior to the pygidium from which it arises comprise the tergite of the tenth segment. The ninth sternite is almost entirely concealed by the eighth tergite and is of an irregular shape; the tenth sternite, bounding the anus below, forms a small projection below the stylet. The genital opening lies between the ninth and tenth sternites.

With the exception of the form of the clasper the parts in *C. felis* conform to the general type found in the Pulicidae. The differences are not so great as to render the parts unrecognizable, if care is taken to mount the dissections in a natural attitude.

Spiracles

The *spiracles* of the flea are regularly arranged. There are three in the thorax, in the positions indicated in the figure, and one between each of the abdominal segments from the second to the ninth. They lie in the soft portion of the tergite, above the middle line of the lateral surface. That of the first abdominal segment lies between the tergite and the epimerum of the metathorax. The spiracular openings are enclosed by rings of chitin, and are easily recognized in cleared preparations.

The vestiture

The arrangement of the hairs or bristles on the integument of *C. felis* is sufficiently indicated in the figure. It will be seen that they are for the most part arranged in regular rows, one to each segment, and that the rows are not placed terminally, but in the middle of the chitinous plate, where the chitin is thickest. There are two rows on the epimerum of the metathorax, and two on the first abdominal tergite. The small eminences of the ninth tergite in front of and below the clasper bear tufts of hairs. As the identification of fleas depends to a large extent upon the arrangement of the hairs every care should be taken to avoid detaching them during the preliminary manipulation of the specimen. If this does happen, the position of the hairs can be judged from the clear spaces which remain at the points of insertion.

The bristle (or bristles) placed at the dorsal angle of the seventh segment is called the *antipygidial bristle.* The number of these is important. There is one pair in the cat flea. The number of hairs on the joints of the legs, and particularly the presence of tufts on the femora and coxae, are also important.

CLASSIFICATION

The Siphonaptera fall naturally into three families, the Sarcopsyllidae, Pulicidae, and Ceratopsyllidae, distinguished from one another both by structure and habits. The first of these families includes the well known 'Jigger' flea, and contains species with a tick-like habit of fixing themselves to their host, a habit which is accompanied by many interesting modifications of their external structure. The majority of known fleas belong to the Pulicidae, of which *Pulex irritans*, the human flea, is the type. In the third family, Ceratopsyllidae, there are two genera, Nycteridopsylla and Ischnopsyllus, which are exclusively parasitic on bats; in these fleas the head is of a peculiar shape, the face sloping strongly forwards and being recurved just above the mouth, with two flaps situated at the frontal oral corner.

The number of new genera and species which have been described within recent years is very great, and it is not possible, within the space available, to give more than a brief account of the more important and interesting forms. In the following the arrangement of the genera is taken mainly from the works of Jordan and Rothschild, and from Baker's papers on the American Siphonaptera.

FAMILY SARCOPSYLLIDAE

Thoracic segments shortened, together shorter than the first abdominal segments in the dorsal line. Genal edge of the head always produced into a triangular process at the ventral oral angle. Rostrum (*labium*) *rather long but weak, consisting of two or three segments, inclusive of the unpaired basal one.*

The Sarcopsyllidae are regarded by Jordan and Rothschild as connected with the Pulicidae, the central family of the order, partly by convergent development and partly by blood relationship. The females, to a varying extent in the different genera, have the characteristic habit of fixing themselves to the skin of the host, and remaining attached in one position for the greater part of their existence, after the manner of ticks; the modifications of external structure which are associated with this habit may be so marked that, in the extreme case of the 'Jigger', all outward resemblance to the other fleas is lost when the female is far advanced in pregnancy. The jigger has, in fact, been mistaken for a mite.

The most striking features are to be found in the head, and show how the insect has become adapted so as to be able to fix itself to its host by means of the mouth parts. The mandibles (Plate LIV, fig. 1) are very much larger and more heavily serrated than are those of the Pulicidae, and recall in a striking manner the fixing mouth parts of ticks. The labium is much thinner and less chitinized, and has the joints reduced to two or three. According to Jordan and Rothschild this is 'in consequence of the females fixing themselves permanently on the host by means of the mandibles and upper lip.' The mouth, instead of pointing downwards, as in the Pulicidae, is directed more forwards, the frontal angle not projecting ventrally. This has brought about a corresponding alteration in the shape of the head, the dorsal border being shortened, and in many, as in *Echidnophaga gallinaceus*, almost flattened in front; the dorsal and the anterior margins meet at an angle, which may be marked by a depression with a tubercle on each side, or by a thickening of the chitin.

It is characteristic of the group that the genal angle of the head is produced to a hook-shaped process, known as the *post-oral process*. This takes the place of the genal comb, and assists the flea in maintaining its hold upon the host.

The thorax is modified in a very characteristic manner, by the shortening of the sclerites which compose the wall until they are together shorter than the first abdominal tergite. The effect of this is to allow of much freer expansion of the abdomen in the female, and to render the insect less liable to be detached from its host. The abdominal sclerites in the male and in the undistended female do not differ much from those of the Pulicidae, but in the pregnant female the normal relations of the parts are greatly altered, and the sclerites separated from one another.

The legs, as one would expect, are only feebly developed, and the claws are small, for the insect does not need them in its sedentary habit of life. The feeble development of the legs may in part account for the reduction of the thoracic segments.

Jordan and Rothschild give the following key to the three genera of the family; altogether fourteen species have been recorded up to the present time.

JORDAN AND ROTHSCHILD'S KEY TO THE GENERA OF THE SARCOPSYLLIDAE

1. Rostrum consisting of two segments. Hind coxa produced into a tooth at apex. Hind femur simple 2
   Rostrum consisting of three segments. Head not divided by a groove or internal thickening from the antennal groove upwards. Hind femur produced ventrally at the base into a prominent hook, behind which the femur is deeply sinuate. Hind coxa without patch of spines on the inner side . . . **Hectopsylla.**
2. Head not divided by a groove or internal thickening from the antennal groove upwards. Thoracic tergites in the dorsal line less than half the length of the first abdominal tergite. No patch of spines on the inner side of the hind coxa. Female without anal stylet . . . . **Dermatophilus.**
   Head divided by a groove or internal thickening from the antennal groove upwards. Patch of spines on the inner side of the hind coxa. Anal segment of female with stylet . **Echidnophaga.**

GENUS DERMATOPHILUS, GUERIN

(Syn. *Sarcopsylla*, Westwood; *Rhynchoprion*, Karsten,
also Baker, 1905.)

This genus contains two species, *penetrans* and *caecata*; Rothschild gives the following key for their identification:—

Eye distinct; head and thorax of pregnant female outside the abdomen . . . . **penetrans.**
Eye vestigial; head and thorax of the pregnant female completely covered by the abdomen, lying in a cavity formed by the latter . . . . **caecata.**

The Jigger Flea

Dermatophilus penetrans, L., is well known under various names, such as 'Jigger', 'Chigoe', 'Nigua', 'Pique', or 'sand flea', as a parasite of man. Apparently it was originally an inhabitant of South America, but on account of its peculiar habit it is well adapted to spread to wherever the climate and local conditions will permit of its existence. It occurs on the west and east coasts of Africa, and has been carried inland from there; it is common in the West Indies, and occurs also in Madagascar. It has been introduced into Bombay and Karachi with infected sailors, but owing to the great care which has been taken to isolate affected persons, and probably also to the damp climate of these ports, it has not succeeded in gaining a footing.

The male and the unimpregnated female behave in the ordinary manner of fleas, and feed on the blood of man and many other animals, domestic and wild ; the pig appears to be a favourite host. The female is much more commonly met with than the male. When impregnated she attaches herself to the skin, boring a way in with the mouth parts, and remains stationary in this position for a week or more, while the ova mature. During this period the abdomen becomes enormously distended (Plate LVI, fig. 4), until the body is the size of a small pea, the head and a part of the neck being just visible at one end and the terminal segments of the abdomen at the other. The swelling is accompanied by great stretching of the integument, affecting mainly the middle segments, the anterior ones being pushed forwards and the posterior ones backwards, so that the wall of the distended portion is chiefly composed of the inter-segmental membrane. When the eggs are mature they are either passed out while the female is fixed to the skin, or the flea may become detached.

The Jigger usually attacks the skin between the toes, though it is not restricted to this region. The presence of the insect gives rise to some inflammation and swelling, which usually fixes it more firmly in the tissues. In some cases severe disability may result from the inflammatory reaction which follows.

The life history, so far as it is known, resembles that of other fleas ; the pupa is enclosed in a cocoon.

Dermatophilus caecata, Enderlein, is a rare or at least a little known species, chiefly of interest because it has been taken on *Mus rattus*. The table already given will suffice to distinguish it from *penetrans*.

GENUS HECTOPSYLLA, FRAUENFELD.

This genus contains four species, all American, of which only one, *psittaci*, Frauenfeld, is at all well known. This species has been introduced into aviaries in Europe with birds, especially parrots, imported from South America. The female differs from the other Sarcopsyllidae in having the sternal plates of the second to the seventh segments divided in the middle line ; when the abdomen is distended by the ripening ova the lateral portions of the plates separate from one another, and are conspicuous on the membraneous wall.

GENUS ECHIDNOPHAGA, OLLIFF.

(Syn., *Argopsylla*, Enderlein, *Xestopsylla*, Baker).

This genus includes several species from Asia, South Africa and Australia, and one from Europe. They occur on many mammals and birds, not being restricted to one host. Several species have been found on rats. One, *E. gallinaceus* (Plate LVI, fig. 3), is the common flea of the domestic fowl, and is found wherever that bird has been introduced.

Echidnophaga is the least specialized genus of the Sarcopsyllidae, the adaptations of structure described above being less marked than in the other genera. The abdomen of the pregnant female does not become very greatly distended, and the sclerites of the abdominal wall are not much separated from one another.

Rothschild gives the following key to the species:—

1. Fifth tarsal segment with three heavy bristles, one small and a long thin subapical hair on each side **2**
   Fifth tarsal segment on each side with one heavy sub-basal bristle, a thinner median one and a small postmedian hair . **liopus**
2. Fifth tarsal segment with two ventral apical bristles; hind edge of head with a lateral lobe . . . . **gallinaceus**
   Fifth tarsal segment with one ventral apical bristle; hind edge of head with a lateral lobe. . . . . . . **myrmecobii**
   Fifth tarsal segment with one ventral apical bristle; hind edge of head without distinct lateral lobes. . . . . . **murina**

All the above have been found on rats. The second species comes from Australia, the third from southern and south-eastern Europe. *E. liopus* was originally found in Western Australia, on *Echidna*. It has also been found in India (Agra) on rats.

FAMILY PULICIDAE

Rostrum more or less strongly chitinized, consisting of five or more segments, inclusive of the unpaired basal one. Thoracic segments together longer than the first abdominal one.

This family contains the majority of the fleas. Many of the species are very little known, and are of no special interest to the parasitologist. The genera may be conveniently, though somewhat empirically, divided into groups, the first of which includes those which have combs on the genal border or on the pronotum, or on both, and may or may not have eyes; the second includes those which have no combs and always have eyes. The latter form a compact series, including the human

PLATE LVI

Figure 1. *Ceratophyllus fasciatus*, ♀. ×36.
Figure 2. The head of *Ctenophthalmus agyrtes*. ×80.
Figure 3. *Echidnophaga gallinaceus*, ♀. ×45.
Figure 4. *Dermatophyllus penetrans*, ♀, in the distended condition, after Taschenberg.
Figure 5. The head of *Lycopsylla novus*, after Rothschild.
Figure 6. *Xenopsylla cheopis*, ♀. ×36.

PLATE.LVI.

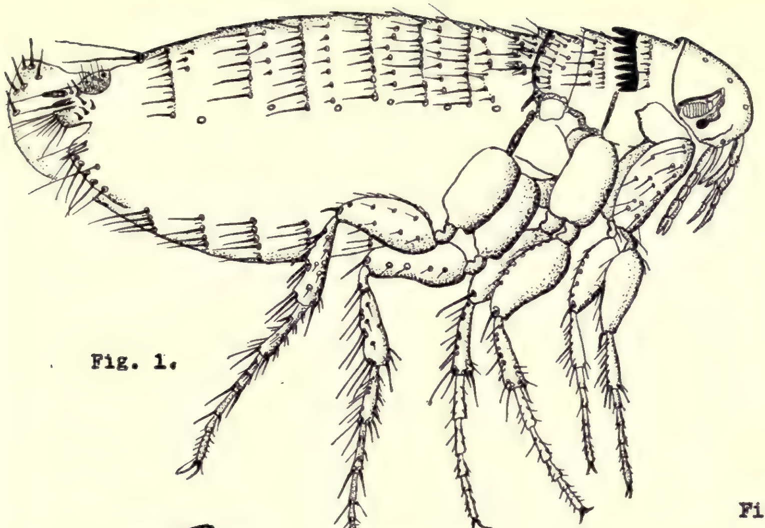


Fig. 1.

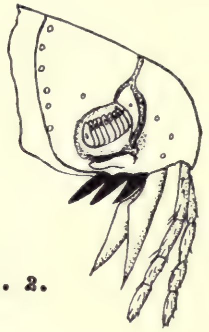


Fig. 2.

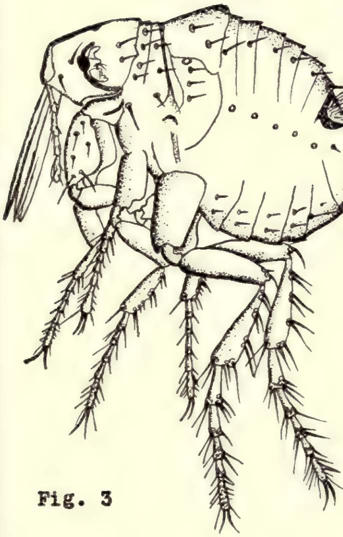


Fig. 3

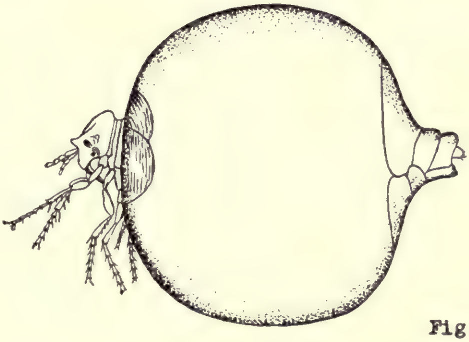


Fig. 4.

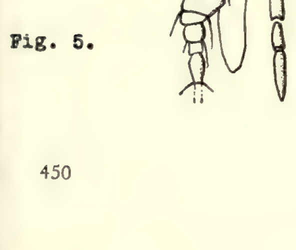


Fig. 5.

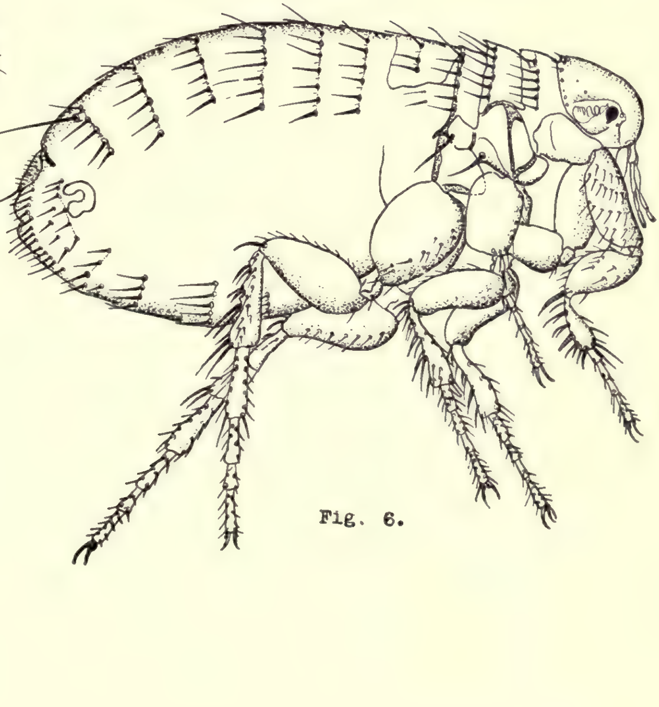


Fig. 6.

flea and the rat fleas of tropical countries, which are of special interest in connection with the spread of plague. These have been exhaustively dealt with by Jordan and Rothschild.

The following key, which is a compilation from the keys of Jordan and Rothschild, Rothschild, and Baker, will serve for the identification of the commoner genera. The first group mentioned above is constituted by the first nine genera, the second group by the remainder.

KEY TO THE PRINCIPAL GENERA OF THE PULICIDAE.

1.	Fleas with or without eyes, and with genal or pronotal comb, or both	2
	Fleas with eyes, and without genal or pronotal comb	10
2.	Club of antenna distinctly segmented only on the hind side	3
	Club of antenna distinctly segmented all the way round	4
3.	With comb on the pronotum only	**Hoplopsyllus.**
	With pronotal and genal comb	**Ctenocephalus.**
4.	Eye developed	5
	Eye vestigial or absent	7
5.	No comb on head	6
	Two spines at angle of gena	**Chiastopsylla.**
6.	Pygidium not projecting backwards. Frons with tubercle	**Ceratophyllus.**
	Pygidium strongly convex, projecting backwards. Frons with tubercle	**Pygiopsylla.**
7.	Abdomen without comb	8
	Abdomen with at least one comb	**Hystrichopsylla.**
8.	Hind edge of tibiae with about eight short and several long bristles, which do not form a comb	9
	Hind edge of tibia with about twelve short and three long bristles, the short ones forming a sort of comb	**Ctenopsylla.**
9.	Fifth segment in fore and mid tarsi with five and in hind tarsi with four lateral bristles	**Neopsylla.**
	Fifth segment in fore and mid tarsi with four and in hind tarsi with three lateral bristles, there being an additional pair in all tarsi on the ventral surface in between the first pair	**Ctenophthalmus.**
10.	Club of antenna short, distinctly segmented only on the posterior side. Antennal groove closed behind, the genal process separating the antennal groove from the fore coxa. Labial palpus consisting of four segments; tip of rostrum asymmetrical. Hind coxa with a comb of spines on the inner side. Antipygidial bristle separate from the apical edge of the seventh tergite	11
	Club of antenna segmented all round, the antennal groove open behind, the genal process being short. Hind coxa without row of spines on the inner side. Labial palpus distinctly segmented all round, consisting of four to seven segments, the tip of the last being symmetrical. One antipygidial bristle, standing at the edge of the segment, which is sinuate.	12
11.	Mesosternite very narrow, without rod-like incrassation from the insertion of the coxa upwards	**Pulex.**

Mesosternite with a rod-like incrassation from the insertion of the coxa upwards . . . . **Xenopsylla.**

12. Club of antenna not symmetrical, the proximal segments sloping backwards. Genal process with only one or two bristles . . . . **Rhopalopsyllus.**

Club of antenna segmented all round, symmetrical. Hind coxa without comb. Antennal groove closed behind. Antipygidial bristle absent in both sexes. Claws of tarsi without distinct basal hook. No anal stylet in female . . . **Lycopsylla.**

GENUS PULEX, L.

Pulex irritans, L., the human flea, is the type and perhaps the only species of this genus. It is found practically all over the world, and though man is the favourite host, it is occasionally found on rats, mice, and other mammals, among which may be noted the badger. It is not the only flea which attacks man, for the cat and dog fleas frequently do so.

A very nearly allied species, which appears to be confined to Mexico, has been described by Baker. Its habit is similar to that of *P. irritans*, from which it may be distinguished by the fact that whereas in the common human flea the labial palpi are one-half the length of the anterior coxae, in *dugesii* they are three-fourths the length or more.

In the early days of the study of fleas a very large number of species were included in the genus *Pulex*, but with a general increase in our knowledge of the family these have been gradually allocated to other genera created for their reception, until now only the two species given above remain, and of these *dugesii* may perhaps only be a local race, the characters distinguishing the two being of doubtful specific value.

Pulex is regarded by Jordan and Rothschild as the most specialized of the Pulicidae, and as approaching nearer to the Sarcopsyllidae than any other. It is undoubtedly an old world form, having spread from its original habitat with civilized man on his travels; it was probably introduced in this way into the New World, with the fleas of which it is not closely allied. Its introduction into some of the more remote parts appears, however, to be of comparatively recent date.

Some diagnostic points other than those given in the key may be useful in distinguishing it in doubtful cases. The mandibles are broad, short, and deeply serrate. The rostrum is shorter than the maxillary palpus, reaching about half-way down the fore coxa. The thoracic tergites are short, each with one row of bristles. The mesosternum (Plate LV, fig. 1) is characteristic, very narrow, its ventral edge strongly oblique, the stigma not covered entirely; there is no rod-like incrassation from the insertion of the coxa to the dorsal edge. The hind coxa is pear-shaped, and bears a number of hairs situated on the inner surface of the posterior portion.

GENUS XENOPSYLLA, GLINK.

(Syn. *Loemopsylla*, Rothsch.)

The palpi are four-segmented; the antennal groove closed, antennae solid in front; the pleura of the mesosternite (Plate LV, fig. 2) divided by a suture into a sternal and a meral portion; the dorsal apical bristle of the seventh abdominal tergite remote from the edge of the segment; there are short spines on the inner surface of the hind coxa, and the division of the rod-like incrassation inside the mid coxa takes place near its base. The clasper of the male has two or three small processes; the manubrium is narrow; the upper internal portion of the ninth sternite is not sharply defined. In the female the stylet bears, besides the long apical bristle, a short bristle situated in a notch before the apex. (Jordan and Rothschild).

This genus derives its importance from the fact that one of the species, *X. cheopis*, has an important relation to plague. It contains in all twenty-four species, most of which are found in Egypt and the Egyptian Soudan, some few coming from Central Asia. They are essentially parasites of rodents, and the plague flea, now found in all parts where the climate is suitable, has been transported from place to place on rats, usually by means of ships.

The following key to the species is from Jordan and Rothschild.

KEY TO THE SPECIES OF XENOPSYLLA

a.	Frontal portion of head with one or two long bristles .	b
	Frontal portion of head with six long bristles	**chephrensis.**
b.	Episternum and sternum of metathorax not separated from each other by a suture; hind femur with or without tooth ventrally at the widest point	c
	Episternum and sternum of metathorax separated from each other by a suture; hind femur with tooth ventrally at the widest point	g
	Episternum and sternum of metathorax separated from each other by a suture; hind femur without a tooth ventrally at the widest point	o
c.	Hind femur with a tooth ventrally at the widest point .	d
	Hind femur without this tooth	**longispinis.**
d.	Fourth segment of hind tarsus short, triangular in outline.	e
	Fourth segment of hind tarsus elongate	f

e.	Middle tergites of abdomen with a row of eight or more bristles on the two sides together	**pallidus.**
	Middle tergites of abdomen with a row of six or less bristles on the two sides together	**somalicus.**
f.	Rostrum reaching to the trochanter	**cleopatrae.**
	Rostrum not reaching to the trochanter	**pyramidis.**
g.	Subapical bristle of the seventh abdominal tergite in ♂ on a conical process which projects beyond the apex of the segment ; seventh sternite of ♀ with about fifteen bristles in front of the postmedian row on the two sides together	**scopulifer.**
	Subapical bristle of ♂ on a process, hind femur in both sexes with three bristles on the outer side	**tortus.**
	Subapical bristle of ♂ not on a process; seventh sternite of ♀ with many less than fifteen bristles ; hind femur with two bristles on the outer side	h
h.	Subapical bristle of seventh abdominal tergite at least as long as the second hind tarsal segment	i
	This bristle considerably shorter than the second hind tarsal segment	n
i.	Epimerum of metathorax with four bristles	**aequisetosus.**
	Epimerum of metathorax with at least ten bristles	k
k.	Longest apical bristle of second hind tarsal segment hardly reaching the base of the fifth segment	**nesiotes.**
	This bristle reaching to the middle of fifth segment or beyond	l
l.	First mid-tarsal segment hardly two-thirds the length of the second	**chersinus.**
	First mid-tarsal segment three-fourths the length of the second	m
m.	Both processes of the clasper slender	**nubicus.**
	One of the two processes broad, its upper edge rounded	**cheopis.**
n.	On the epimerum of the metathorax at least one bristle situated above the stigma	**niloticus.**
	All the bristles of the epimerum of the metathorax ventral to the stigma	**eridos.**
o.	Hind coxa pear-shaped, the comb situated near the apex	p
	Hind coxa more or less sinuate behind near the apex	r
p.	Rostrum shorter than the maxillary palpus	**creusae.**
	Rostrum longer than the maxillary palpus	q
q.	Apical margin of the seventh abdominal tergite strongly chitinized dorsally, projecting backwards	**divergens.**
	This portion of the segment hardly more chitinized than the rest of the segment, projecting very slightly backwards	**isidis.**
r.	Rostrum reaching beyond the trochanter	**erilli.**
	Rostrum at the most reaching to the apex of the fore coxa	s
s.	Rostrum shorter than the fore coxa	t
	Rostrum extending to the apex of the fore coxa	**regis.**
t.	First hind tarsal segment with five apical bristles which extend to the apex of the second segment or beyond	**gerbilli.**

First hind tarsal segment with less than five bristles which reach to the apex of the second segment . . . . u

u. Rostrum longer than the maxillary palpus . . . . . **mycerini.**

Rostrum as long as the maxillary palpus ; upper process of the clasper (♂) broad, truncate . . . . . . **ramesis** (and **conformis**).

Of these, all have been found in Egypt except *creusae* and *scopulifer*, which are South African. *Nubicus* was taken on *Mus macleari* on Christmas Island.

The synonomy of *cheopis* is as follows. *Pulex cheopis*, Rothschild, 1903. *P. brasiliensis*, Baker, 1904. *P. murinus*, Tiraboschi, 1904. *P. philippinensis*, Herzog, 1904. It used to be referred to as *Pulex pallidus*, Tasch., in plague literature. The figures on Plate LV will assist in the identification of this species.

GENUS RHOPALOPSYLLUS, BAKER.

This genus is exclusively American, and includes fleas found mostly on small rodents, such as weasels, opossums, peccaries, and ground squirrels. Some of them may prove to be of importance in connection with plague in the localities in which they occur.

GENUS LYCOPSYLLA, ROTHSCHILD.

This genus, for which a new family has been proposed by Baker, is distinguished from *Pulex* by the presence of a small sinus on the front of the head (Plate LVI, fig. 5), closed in anteriorly by a distinct tooth. The seventh abdominal tergite has no apical bristle. One species, *novus*, Rothschild, is known, from the Australian Wombat, *Phascolomys mitchelli*.

GENUS HOPLOPSYLLUS, BAKER.

A genus of North American fleas, mostly occurring on rabbits, though on one occasion *H. anomalus* has been found on a rat. Baker gives its host as *Citellus* (ground squirrel, California). The genus resembles *Pulex*, but is sharply distinguished from it by the presence of the pronotal comb.

GENUS CTENOCEPHALUS, KOLENATI.

In this genus are contained the cat and dog fleas, frequently confounded with one another, or regarded as the same species. The distinction may perhaps prove of interest in connection with Kala Azar. The points on which they are separated by Rothschild are as follows. In

Ctenocephalus felis,* Bouché, the cat flea, the head of the female is long and pointed, while that of the female of *C. canis*, Curtis, is more rounded. The difference in contour is less marked in the males, but is present. In each species there are eight spines on the genal comb, but in both sexes of *canis* the first spine and the one at the genal angle are shorter than the corresponding ones in *felis*. The hind tibia of *canis* bears two bristles at the edge, situated between the fifth and the dorsal apical pairs, while in *felis* there is only one bristle and a small hair in this situation. The mid-tarsus of *felis* is more slender and the second segment narrower than in *canis*. The males can be distinguished by the structure of the ninth tergite. The clasper or 'moveable finger' of *felis* bears more hairs than that of *canis*, and in the latter the manubrium is slightly swollen (Plate LIV, fig. 3). In addition to these characters, the number of bristles on the metathoracic episternum, the epimerum, and the inner side of the hind femur, is slightly greater in *canis* than in *felis*.

Both species are said to be widely distributed and common, though little seems to be known with regard to the relative frequency of their occurrence. It is by no means the case that *canis* is found on the dog and *felis* on the cat, for they both occur on either animal and on many others beside, notably on the various species of rats which frequent the same localities. Both will bite man on occasion. In Madras the common flea on the street dogs is *C. felis*, while *canis* occurs on the jackal. According to Mr. Rothschild, *canis* is more abundant in temperate countries than in the tropics.

GENUS CERATOPHYLLUS, CURTIS.

This is a very large and widely distributed genus, the species of which are found chiefly on rodents and other small mammals, some also occurring on birds. Many of the species are found on moles, and in America on squirrels and ground rats. The important forms are those which have been found on rats and house mice. Of these *C. fasciatus* is the common flea found on rats in Europe, while *C. penicilliger* is common on field mice in England. *C. fasciatus* can be distinguished by the shape of the moveable process of the clasper, the proximal edge of which is angulate, and by the sinuous edge of the seventh abdominal sternite. It has eighteen to twenty spines on the pronotal comb. *C. acutus*, Baker, is the common flea of the Californian ground squirrel.

Further distinguishing characters of the genus are as follows. Three antipygidial bristles on each side. No comb of minute teeth on the inner side of the hind coxa. The last joint of the hind tarsus has five pairs of lateral spines, all in a line or only the last pair slightly dislocated.

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* The cat and dog fleas are frequently called *Ctenocephalus (Pulex) serraticeps felis*, and *C. serraticeps canis*. This is incorrect; the name *serraticeps* should be dropped.

GENUS PYGIOPSYLLA, ROTHSCHILD

This genus is distinguished from *Ceratophyllus* by the marked convexity of the pygidium. Fifteen species are known, mostly from the tropics. Of these *hilli*, Rothsch., and *rainbowi*, Rothsch., have been found on *Mus rattus*, though their normal host appears to be *Mus assimilis*, on which they occur, together with *P. gravis*, in Australia.

GENUS CHIASTOPSYLLA, ROTHSCHILD

This genus includes three South African species, one of which, *Ch. rossi*, has been taken on a rat. The genus is distinguished from *Ceratophyllus* by the presence of two spines at the genal edge of the head, one lying on top of the other, and by the presence of one antipygidial bristle on each side. The hind coxa has a comb of spines on the inside, and the mid and hind femora bear no lateral rows of bristles.

GENUS NEOPSYLLA, WAGNER

One species, *N. bidentatiformis*, Wagn., has been found on a rat in Russia.

GENUS CTENOPTHALMUS, KOLENATI

This is also a large genus, the species of which are widely distributed. In addition to the structural features given in the key, the genus is distinguished as follows. The genal comb consists of fewer teeth than in *Ctenocephalus.* Midway between the palpi and the antennal groove there is a distinct frontal tubercle situated in a groove. There are three antipygidial bristles on each side. *Ct. agyrtes* is common on field mice in England, and is found also on *Mus norwegicus*, when captured in the open country. It has three teeth in the genal comb, and sixteen on the pronotum. *Ct. assimilis* occurs on field mice in Central Europe, and has also been found on rats. It has three teeth on the genal comb and sixteen on the pronotal one.

GENUS CTENOPSYLLA, KOLENATI

This genus presents such marked characteristics that Baker has proposed to place it in a separate family, the Ctenopsyllidae. The most striking feature is the shape of the head, which is pointed anteriorly, the angle being situated not far in front of the antennal groove. As a result of this retroflection of the anterior and dorsal part of the head the genae are almost vertical, and the antennal groove almost horizontal instead of oblique. Both genal and pronotal combs are present. On the hind edge of the tibia there is a close set row of bristles resembling a comb.

One species, *C. musculi*, is a common flea of rats and mice, and has become cosmopolitan in consequence. It is distinguished by having four spines in the genal comb, and two bristles near the front angle of the head which resemble the spines of the comb.

GENUS HYSTRICHOPSYLLA, TASCHENBERG

This genus is also very distinct, and has been placed in a separate family, Hystrichopsyllidae, by Tiraboschi. The abdominal tergites, as well as the genae and the pronotum, may bear combs. The number of spines in the pronotal comb may be very large, and the integument as a whole is very hairy. One species, *H. tripectinata*, occurs on rats and mice in the Mediterranean. In this the genal comb is limited to the lower edge of the gena, the first abdominal tergite only bears a comb, and the remaining tergites have some small spines.

LIFE HISTORY AND BIONOMICS

Fleas pass through a complete metamorphosis comparable with that of Diptera, from egg, larva and pupa to imago. Each stage resembles the corresponding one in the Diptera. The life history of only a few species has been followed out, and little or nothing is known regarding the variations which may exist in the different genera. Most of the observations have been made on those fleas which are connected with rats and plague.

Metamorphosis: Life history of Ctenocephalus felis

The following applies to *Ctenocephalus felis*, which is comparatively easy to rear in the laboratory and to observe in its natural habitat. The *eggs* (Plate LVII, fig. 16) are minute oval bodies of a pearly white colour, just visible to the naked eye. They are deposited by the flea in places where the host is in the habit of sleeping, either by day or by night, and are not attached to the surroundings in any way, but simply dropped on the ground or bedding near the host. About a dozen or a little more, judging from the examination of the ovaries of apparently mature females, are laid at one time. It is not often that the flea will lay all its eggs in a tube, where they may be counted. The number which may be deposited by the fleas of a single host in a night is enormous. One of the writers once saw the inside of a hat, in which a kitten had spent the night, so covered with them that it looked as if it had been sprinkled with sugar by a sifter. The eggs hatch in from two to four days, according to the temperature.

PLATE. LVII.

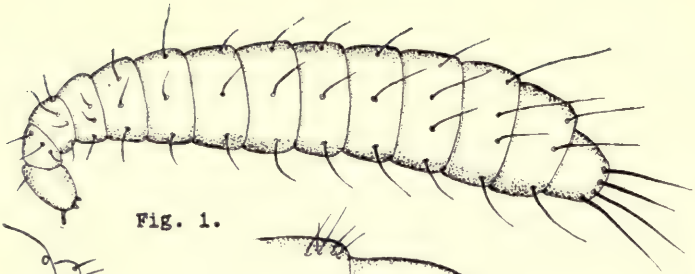


Fig. 1.

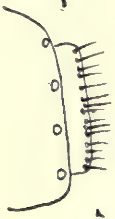


Fig. 2.

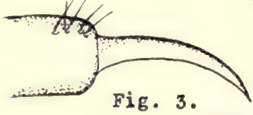
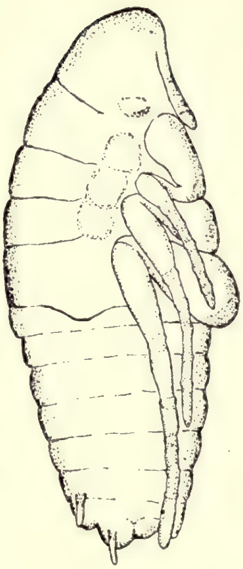


Fig. 3.



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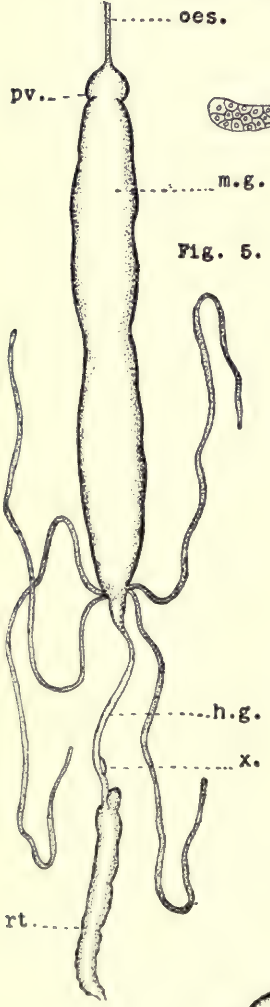
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h.g.
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Fig. 5.

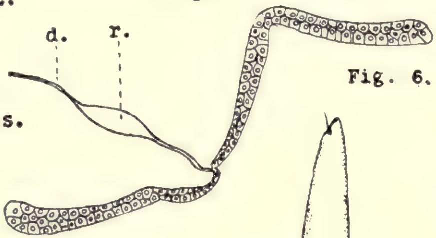

Fig. 6.

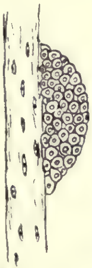

Fig. 7.

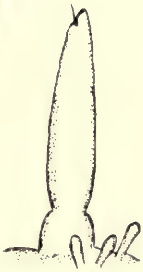

Fig. 8.

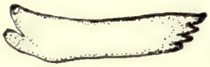

Fig. 9.

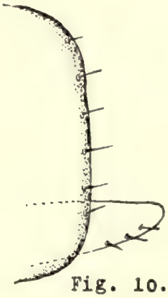

Fig. 10.

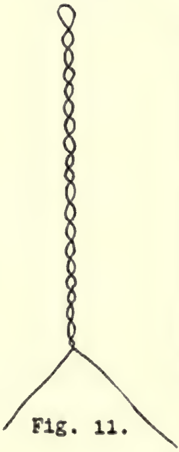

Fig. 11.

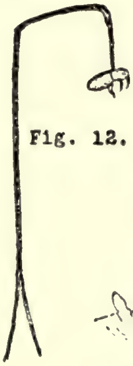

Fig. 12.

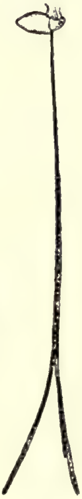

Fig. 13.

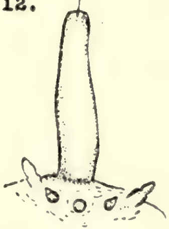

Fig. 14.

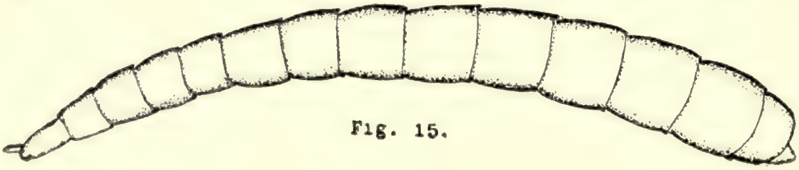

Fig. 15.

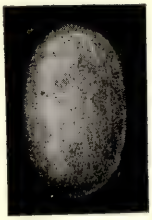

Fig. 16.

PLATE LVII

Figure 1. The larva of *Ctenocephalus felis.* × 28.
Figure 2. The terminal segments of the same.
Figure 3. The anal process of same.
Figure 4. The pupa of *Ctenocephalus felis*, removed from its cocoon.
Figure 5. The alimentary tract of the larva of *Ct. felis.*
Figure 6. The salivary glands of the larva.
Figure 7. The mass of cells on the wall of the hind-gut, marked x in figure 5.
Figure 8. The antenna of the larva of *Ct. felis.*
Figure 9. The mandible of the larva of *Echidnophaga gallinaceus.* Note the serrated border.
Figure 10. The terminal segments of the larva of *E. gallinaceus.*
Figure 11, 12, and 13. The 'circus' method of controlling single fleas for experimental purposes, after Nöller.
Figure 14. The antenna of the larva of *Echidnophaga gallinaceus.*
Figure 15. The larva of *Echidnophaga gallinaceus.* × 28.
Figure 16. The egg of *Ct. felis.*

PLATE LVI

The larva

The *larva* (Plate LVII, figs. 1, 2, 3 and 8) is a minute maggot-like creature, bearing a strong superficial resemblance to a Dipterous larva. It moves about actively in dust or sand,* and is best recognized by shaking up the debris and watching for moving particles, as it usually keeps below the superficial layer. It consists altogether of fifteen segments, including the head and the hidden terminal segment. Of these the posterior are the largest, the posterior half of the body being distinctly thicker than the anterior, though there is not quite that tapering appearance seen in the Muscid larvae. The segments are rounded, and there are no pseudopodia or legs. The head is small and conical, and bears a pair of simple cylindrical and tapering antennae, at the apices of which there is a minute hair. The base of the antenna is set on a small raised area at the side of the head, dorsal to the mouth, and has around it a row of five or six minute conical and apparently jointed processes. Each of the succeeding segments down to the tenth bears a row of six minute hairs, inserted in the middle of the length of the segment, and increasing progressively though not markedly in length from before backwards, as the segments themselves increase in size. The eleventh and twelfth segments bear eight hairs each; of these the twelfth is the largest of the body, and bears the longest hairs. The thirteenth segment has six hairs, and is considerably smaller than the preceding ones. The fourteenth segment is still smaller, and has on each side a row of four hairs which are rather stouter and longer than the rest, and are placed on the distal margin of the segment. The fifteenth segment is very small, and is concealed by the one in front of it. It bears terminally a row of fifteen minute hairs on each side. Projecting from within the last segment there is a pair of minute slightly curved and elongate pointed processes, arising from a stouter base.

Internal anatomy of larva

The internal anatomy of the larva is simple, and strongly resembles that of the adult—to a much greater extent than is found in the Diptera. The *alimentary canal* (Plate LVII, fig. 5) commences as a narrow oesophagus, which after a short course joins a small conical proventriculus. The main portion consists of a sausage-shaped mid-gut, about seven times as long as wide, which passes straight down the body without convolutions. The four Malpighian tubes are inserted at its posterior end; these do not differ from those of the adult. The remainder of the gut is coiled up in the last segments of the body. It consists of two distinct portions of approximately equal length, the first of which is very narrow, little wider in fact than the oesophagus, while the second and terminal part, which may be taken as the rectum, is wider. The narrow part of the hind gut has on it near its termination a small clump of round cells (fig. 8), of unknown function and origin, placed at one side. This portion does not become directly continuous with the rectum, but joins it a short distance from its anterior end. The wall of the rectum contains many muscular fibres, arranged obliquely. There are no rectal papillae.

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* It can also move actively on glass or smooth paper.

Salivary glands of larva

The *salivary glands* (Plate LVII, fig. 6) also present a remarkable similarity to those of the adult. There are two glands on each side; they are tubular, elongate, slightly swollen at the blind ends, and join one another at their narrow ends without intervening ducts. From their point of union a fine salivary duct arises, and passes to the mouth, near which it unites with its fellow from the opposite side. About midway on the course of each of the salivary ducts there is a fusiform dilatation, equal in width to the widest part of the gland. The walls of the glands are formed of a single layer of cubical cells, surrounding a central lumen. The wall of the dilatation on the duct, on the other hand, is extremely thin, and contains only a few very small and flattened cells, its structure suggesting that it functions as a reservoir.

Food of the larva

The food of the larva is something of a mystery. In a large proportion of the larvae which the writers have examined the intestine has contained blood, in stages varying from fresh unclotted blood to particles of blood pigment; the dark colour of the living larva is due to the presence of this material. Similar observations have been made on the larva of *Xenopsylla cheopis*, *Ceratophyllus alladinis* from the Indian squirrel (*Funambulus palmarum*), and in an undetermined species from *Gerbillus indicus*, so that the circumstance is by no means peculiar to the cat flea. It has never been suggested that the larva is a blood-sucker, and it has no biting mouth parts; the most probable source of the blood is the adult flea. It is well known that the flea, like most blood-sucking insects, has the habit of defaecating while feeding,[*] or shortly after; not only is the hind gut emptied on these occasions, but fresh red blood is passed, the insect appearing to take up more food than it can digest. In this way blood is passed in considerable quantities among the debris under the host, and is ingested by the larva. Whether blood so obtained constitutes the sole or the main food of the larva, or whether it is simply taken in when met with, it is impossible to say, but of the actual presence of fresh mammalian blood in the gut, often in a large amount, there is no doubt.

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[*] Nöller, experimenting with the dog flea, found that the insect defaecated from seven to fifteen times during a feed lasting two and a half to three and a half hours, the last material voided being red fluid blood. *Pulex irritans* was found to defaecate ten to twenty times in half an hour.

Regarding the length of the larval stage exact data are not available, as it is a matter of great difficulty to separate out the eggs of one batch. It appears, however, to be about ten days, rather longer in cold weather, in *C. felis* and *X. cheopis.* At the end of this time the larva spins for itself a cocoon like that of many Lepidoptera, covering the outer wall with fragments of the debris among which it lies. The pupal cases so formed are minute oval bodies, looking just like collections of sand granules stuck together by moisture. When they are opened, as can easily be done with a pair of sharp needles, the ***pupa*** (Plate LVII, fig. 4) is found lying free within. When nearly mature it resembles the adult; the legs and palps lie folded against the body, and the head is bent ventrally. It is white in colour, and the segmentation of the exo-skeleton can be easily made out. At the posterior end there are two pairs of short processes, on the last and penultimate segments respectively, the nature of which has not been determined. The duration of the pupal stage is normally seven to ten days.

The larvae of *Xenopsylla cheopis* and *Ceratophyllus alladinis* resemble those of *C. felis.* That of *Echidnophaga gallinaceus* (Plate LVII, fig. 15), on the other hand, simulates a Muscid larva more closely; the body is longer and tapers more towards the anterior end, and has on it only a very few short hairs. The alimentary canal is also longer and more coiled. Specimens which have been examined by the writers, and from which the imagines were bred, do not conform to the description of the larva of *Dermatophilus penetrans* as given by Newstead, as one would expect from the close relationship of the two genera.

Bionomics—Relation to host

As is the case with most ectoparasites, each species of flea has a particular host, the blood of which is its normal food. But the relation between the different species of fleas and their hosts is not a close one, and in the absence of their ordinary food most of them will feed readily enough on the blood of other hosts, either allied species or widely separated ones. In Madras, for instance, the flea which commonly attacks human beings is *C. felis*, ordinarily found on the cat and dog. *P. irritans** has not been met with in the plains, while the cat flea is common everywhere when domestic dogs and cats are kept. It has been shown experimentally by several observers that *X. cheopis* will attack man in the absence of its ordinary host. Many of the fleas collected during the researches of the Indian Plague Commission were obtained by placing guinea pigs in infected houses.

Chick and Martin have performed some exact experiments to determine the readiness with which certain fleas attack man, and have shown that when starved for varying periods and then placed on the arm in a test tube, *Ceratophyllus fasciatus* feeds readily, more than half the experiments proving successful even under these artificial conditions. *Ctenopsylla musculi*, on the other hand, will rarely bite man, while *Ctenophthalmus agyrtes* will not do so at all. The latter flea, it should be noted, lives on field mice, not on the rats and mice which frequent human habitations, and will therefore seldom come into contact with human beings. *Ceratophyllus acutus*, the flea of the Californian ground squirrel, will feed on man.

The Indian rat flea, *X. cheopis*, attacks man readily, and its inclination to do so in the absence of a sufficient number of rats for the flea population is one of the factors in the rôle which it plays in the transmission of plague. The Jigger flea has been found on a large number of hosts, and *Echidnophaga gallinaceus*, which is normally a parasite of the domestic fowl, will attack rats which frequent the hen houses, and will also bite man. A certain catholicity of taste is the rule among the Siphonaptera, a fact which is well brought out by the lists of hosts given by Jordan and Rothschild, and by Baker, for the less known fleas.

Method of feeding

The method of feeding can be readily observed in fleas which have been starved for a day or so and then placed on the arm; they can be watched during the process under a hand lens. After the usual investigation, in which the maxillary palps appear to take a part, the flea settles down and presses its head against the skin, tilting its abdomen in the air in a way that reminds one forcibly of the attitude assumed by many Diptera. As the head is pressed to the skin the labial palps can be seen to diverge from one another. In a favourable light, and with a binocular microscope, one can see the blood passing rhythmically into the abdomen. The flea does not as a rule take much notice of the observer, and one notes that the pain of the bite is not felt during the time the mouth parts are being driven in, but after a short interval, when the blood has begun to flow; from this it may be inferred that it is the saliva which causes the irritation, and not the puncturing stylets.

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* According to Gimlette, *Pulex irritans* is unknown to the Malays of Kelatan, though they recognize the dog flea.

The common observation that some individuals suffer more from the bite of the flea than others was borne out in a curious manner by the experiments of Chick and Martin. In these eight human hosts were tried; in seven little or no irritation was produced, while in one quite severe inflammation was set up around each bite. The bite of *Cr. fasciatus* and of *Ct. felis* is not nearly so irritating to most people as that of *Pulex irritans*.

Whether fleas spend the whole or nearly the whole of their lives on the skin of the host, or whether they habitually leave it for digestion, has not been determined with accuracy. In the dissection of fleas (e.g. *Ct. felis*) one finds them at all stages of digestion and with ovaries containing ova at all stages of maturation, even when dissected immediately after removal from the body of the host. In the examination of nests both of birds and mammals one finds as a rule larvae and pupae only, and very few imagines. On the other hand, the human flea appears to leave its host when it has fed. The females must, of course, in all cases leave the body to deposit their eggs.

Like all other blood-sucking insects, fleas leave the body of the host immediately on the death of the latter, and seek out a fresh host. Should one of the proper species not be available, as may be the case when an epizootic of rat plague has occurred, the fleas will attack an abnormal host, which, in this case, may be man.

The fleas found on rats

From what has already been said with regard to the choice of host, it will be evident that one may expect to find many species of fleas on the rat in addition to those which are normally its parasites. *Pulex irritans*, for instance, is occasionally, though rarely, found on the rat, and *Echidnophaga gallinaceus* on rats which have been captured in hen houses. The cat and dog fleas are found on rats which have lived in places where these animals are kept.

Long lists have been compiled of the species which have been taken on rats, but many of these have been recorded only once or twice, and are of no practical importance. The following are the species commonly met with.

Xenopsylla cheopis. The common rat flea of the tropics.

Ceratophyllus fasciatus. The common rat flea of the colder parts of Europe, but found also in the tropics in the colder parts of the year.

Ceratophyllus anisus. Represents the above species in Japan.

Ctenopsylla musculi. The flea of the house mouse, *Mus musculus,* but occurring also on rats.

Ctenopthalmus agyrtes. The flea of the field mouse and vole. It is also found on rats living in similar situations.

Some idea of the proportions of these species found in different localities may be obtained from the following table, taken from the Reports of the Indian Plague Research Commission. It has been compiled from a large number of records made by different observers.

		Percentage of total fleas belonging to each species.					
——	Fleas examined	*Xenopsylla cheopis*	*Ceratophyllus fasciatus*	*Ceratophyllus anisus*	*Ctenopsylla musculi*	*Ctenopthalmus agyrtes*	*Other species*
India	891,000	100	trace	...	...	...	...
Australia ...	2,000	63	11	...	24	...	2
San Francisco.	31,000	28	58	...	8	...	6
Japan	8,000	18	...	46	24	...	12
Mediterranean.	13,500	58	25	...	11	...	6
England ...	1,000	...	48	...	...	52	...

The figures given above probably exaggerate the prevalence of *cheopis,* as this species is specially common on rats taken in the neighbourhood of shipping, where most of the counts were made. Slight differences in the locality from which the rats were taken may make considerable alterations in the proportions of fleas present, on account of the change in the environment of the host.

Different species of fleas appear to select different regions on the body of the host, a point which is well brought out by counts of rat fleas, mainly from *Mus norvegicus,* made by McCoy and Mitzmain in California, as shown in the following table :—

	fasciatus	*cheopis*	*musculi*
Head and Neck ...	3·3 per cent	7·7 per cent	87·2 per cent
Fore Quarters ...	10·5 ,,	6·8 ,,	12·2 ,,
Hind Quarters ...	86·2 ,,	85·5 ,,	·6 ,,

Most of the fleas on dogs and cats are found about the abdomen. The flea of the Indian squirrel is generally found about the rump. In the case of the rat flea it is suggested that the site in which the fleas are found may be related to the usual site of the plague bubo.

Seasonal prevalence

The seasonal prevalence and reproduction of fleas are markedly affected by conditions of temperature and humidity. The conditions have been carefully studied in connection with the seasonal incidence of plague, since it was found that the period of the greatest prevalence of the rat flea is also the season of the maximum intensity of the disease. The average number of fleas per rat (*cheopis*, almost without exception) in Bombay varies from 6·7 and 6·8 in March and April, the height of the plague season, to 2·9 in October; in the Punjab an average of 12·6 has been found in April, which is the beginning of the hot weather and the time of the heaviest mortality from plague, as against an average of 2·0 in August, when the disease is dying out. Similar results have been obtained in Australia.

The prevalence of *Ceratophyllus fasciatus* is the reverse of the foregoing, so far as India is concerned. It is found only rarely at any time, and seldom amounts to more than two per cent of the total in the Punjab districts, and it only occurs in the early part of the cold weather, disappearing entirely as the hot weather comes on and the percentage of *cheopis* increases. *Ct. felis* is present in the greatest numbers in Madras in November and December, two fairly cool months. *Echidnophaga gallinaceus* has been found breeding in enormous numbers in the hot weather in the hills in South India, but could not be found in the same place in the cold weather. For every flea, apparently, there is an optimum temperature for reproduction, as is the case with so many other insects.

Length of life

The length of life of the flea, and the duration of the several instars, are still matters of dispute, and the observations so far recorded suggest that these insects are very remarkable in this respect. It has been frequently observed that fleas (*P. irritans?*) have appeared in enormous numbers in places which have not been visited by man for very prolonged periods, and that, even in towns in Europe, they are often very numerous and voracious in houses which have not been occupied for some time. Some exact observations have been made with *Ceratophyllus fasciatus*. Nicoll found that the average length of life at ordinary temperatures was six to eight days, with a maximum or over forty days in one experiment. Ten per cent lived over fourteen days. The average duration of life is much greater in winter than in summer, and at very low temperatures (0°–8° C.) they may be kept alive for two months. He also found that under certain circumstances the larval and pupal stages might be prolonged for as much as a year, so that even after the removal of the adult fleas and the host from any place which has been infected, imagines may continue to appear at intervals for a considerable time, as long as fourteen months in one case. Strickland, who has worked on similar lines, is of the opinion that the persistence of the imagines is not due to a succession of individuals emerging from the pupae, but to the actual survival of the original fleas for very long periods without food—in one case for at least eighteen months. Bacot, on the other hand, under the most favourable conditions which he could devise, could not keep adult fleas alive for longer than ninety-five days, and attributes the persistence of the insects in breeding cages after the removal of the host to the long period which may elapse between the time at which the larva becomes full fed and emergence from the pupal case. He found that, after spinning its cocoon, the larva may rest within it for a varying length of time, as much as four hundred days; the pupal stage is about ten or twelve days, but even after the imago has shed its pupal skin it may still rest for a time within the cocoon. He states that the eggs hatch after four to twelve days, according to the temperature, and that the active life of the larva may be anything from ten to a hundred and fourteen days or more.

Unfortunately only preliminary notes * of the work of these observers have as yet appeared. The detailed accounts will be awaited with interest.

The experiments of the Indian Plague Commission with *X. cheopis* have not revealed any evidence of a similar longevity. They found that this species, if removed from the host, will live for several days if kept in bran, sacking, rice, etc., and from eight to fourteen days if kept in sand which is slightly moist. When in association with their normal host, the rat, six per cent were found alive on the forty-first day, suitable precautions having been taken to prevent reproduction from vitiating the experiment. When fed on human blood some were found alive after twenty-seven days, and after twenty days when fed on the blood of a guinea pig. A similar shortening of life has been observed in *Pulex irritans* when removed from its normal host.

As a general rule excessive light, dryness, and heat are inimical to fleas, and a moderate degree of humidity advantageous. Fleas which have not fed since they emerged from the cocoon will survive longer than those in which adult life has properly commenced. Specimens removed from the host and kept in glass tubes usually die in a few hours.

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* *British Medical Journal*, October 26, 1912, May 31 and June 14, 1913.

Breeding and Manipulation

The following method for breeding the fleas of small animals is at once simple and effective. The animal is either caught in a wire trap, or subsequently placed in it, together with its nest or some soft hay or other debris, and the whole is wrapped round in a large piece of stout white cloth, tied up at the top. Food is introduced through the door of the trap. Any urine passed by the animal is at once absorbed by the cloth, so that the surroundings are always kept dry. Faeces will usually pass through the bars, and can be removed. When the cloth becomes dirty the cage and all the debris under it are lifted up and removed to a clean one. The eggs of the flea are laid on the cloth, and the larvae make no attempt to move away, and can at any time be picked out from the debris under the cage. If it is desired to examine the animal closely it can be removed by hand through the door of the cage, taking the precaution to wrap the hand in a piece of cloth. This method has the great advantage that the material under the animal never gets sodden with urine. The fleas never attempt to leave the host. For exact experiments the possibility of other fleas reaching the animal from outside can easily be guarded against.

Fleas may also be bred in larger cages fitted with a lattice-work false bottom, on which the host rests. Under this is placed a tray of sand, previously sifted and cleaned, and if necessary sterilized by heat to kill off any eggs which may be present. The females leave the host to oviposit in the sand, from which the larvae and pupae may be obtained. In searching for larvae one may either rake the sand with a needle, when they will betray their whereabouts by their movement, or else spread out a quantity of the sand on a large sheet of white paper and examine it, if necessary, with a hand lens. If the sand is spread out in a thin layer the larvae leave a track behind them as they move about, thus rendering detection easy. Pupae may be collected from the sand under the host by passing it through a fine sieve; or they may be found in little heaps, the cocoons adhering together, in corners of the tray.

Larvae should be picked up with a small moist brush, never with forceps.

If the number of fleas found naturally on each host is small, all the fleas from several hosts should be transferred to one experimental animal, preferably a young one. This is best done by chloroforming the hosts, and removing the fleas by means of a fine comb. If they are placed in the cage with the future host they will pass on to it as soon as they recover from the anaesthetic.

Manipulation of single Fleas

Minchin and Thompson, in their experiments with the rat flea as a transmitter of *Trypanosoma lewisi*, in some of which only one flea was used for each animal, used 'specially constructed 'rat cages, each consisting of a tin cylinder, 6 in. in 'diameter, 10 in. in height; the bottom is closed in 'with tin, the top with a tightly fitting tin cover, which has an opening 'sufficiently wide to admit air for the rat, but barred doubly with both 'wire gauze and finely meshed cloth gauze, the former to prevent the 'rat forcing its way out, the latter to make it flea proof.' Some sawdust was placed at the bottom of the cage, and the rat kept in it during the period of the experiment. A single flea could be recovered from the rat, or from the sawdust.

Nöller, in his elaborate and exact experiments on the transmission of *Trypanosoma lewisi* by the dog flea, adopted the method in use by keepers of performing fleas. The flea is enclosed in a loop of fine silver wire, ·1 mm. thick, passed around its thorax between the second and third pairs of legs, the free portion of the wire being twisted into a spiral to serve for a handle. The fleas are thus secured at the commencement of the experiment, and remain under perfect control while they are fed. In the intervals between feeds they are kept, still fastened to their wire handles, in open Petri dishes, between two layers of cotton wool.

The cages used by the Indian Plague Commission for the demonstration of transmission of plague from rat to rat were constructed as follows. A wire cage about 12 cm. in diameter and about 8 cm. high, having a mesh of ·1 mm., contained the rat. This was attached below to a tray containing sand or dry earth. The upper side was completed by a cylinder of metal, 15 cm. high and 9 cm. in diameter, the upper end of which was covered with a lid. Two of these cages were enclosed in a glass box, the top of the whole being covered with fine muslin, of a mesh through which fleas could not penetrate. The top of the lid, which had an aperture for the supply of air to the rat, was also covered with muslin. In this way the two rats could not come in contact with one another, nor with the urine or faeces, but fleas could pass readily through the wire-work of the lower part of the cages, and could therefore pass from rat to rat. Both cages are protected against the entrance of other fleas by the muslin which envelopes the whole.

THE INTERNAL ANATOMY. (Plate LVIII)

The internal structures of the flea are comparatively simple, and resemble those of the Diptera.

The alimentary canal

The alimentary canal (Plate LVIII, fig. 3) may be divided into pharynx, oesophagus, proventriculus or gizzard, mid-gut or stomach, hind-gut, and rectum. With the exception of the proventriculus these parts resemble the corresponding ones in the Nematocerous Diptera.

The *pharynx* is a chitinous chamber situated dorsal to the antennae in the head. It is somewhat spindle-shaped and elongate, but is expanded more on the dorsal than on the ventral side. It consists of two chitinous plates, a dorsal and a ventral. The dorsal plate is continuous with the epipharynx and the ventral with the hypopharynx, as in the Diptera, but in the case of the latter organ the chitinous portions of the two laminae are separated by a layer of fibrous tissue, in which the salivary duct lies. Posteriorly the pharynx tapers off at the hind portion of the head to become continuous with the oesophagus. The dilator muscles pass between the dorsal plate and the wall of the head cavity, and are separated into several discrete bundles. The oesophagus is extremely thin, and has a wall consisting almost entirely of thin and flexible chitin, with few cells and no muscular tissue. It extends as far as the posterior limit of the thorax.

The *proventriculus* is a remarkable organ, the function of which is obscure. It is a short conical or button-shaped body, situated between the oesophagus, the posterior end of which is dilated at the point of junction, and the mid-gut, and guards the entrance to the latter. From its inner surface there arises a close-set series of long chitinous rods (figs. 4 and 8), which pass first inwards and slightly backwards towards the middle of the lumen, those from all parts of the periphery converging towards one another, and then turn sharply backwards towards the lumen of the mid-gut, into the anterior portion of which they project. The rods are rounded on section, but are closely compressed together at the base, so that they become hexagonal and produce a pattern on the wall like that of the facets of the compound eye of Diptera. In longitudinal sections of the organ they form a lattice pattern, due to the crossing of parts of rods in front of and behind the bend.

The function of this arrangement of rods appears to be to prevent the regurgitation of the contents of the gut when the pharynx is dilated in the act of sucking, and to compensate thereby for the lack of muscle in the wall of the oesophagus. It is analogous, therefore, with the proventriculus of *Musca*. Probably when the muscles of the pharynx contract the negative pressure so produced first closes the lumen of the proventriculus by drawing the rods in contact with one another. The wall of the proventriculus itself has no muscular tissue.

The *mid-gut* is an elongate oval body, widest posteriorly, and forms by far the largest part of the alimentary tract, extending to the hind end of the body. Its wall consists of a layer of muscle fibres, more irregularly arranged than is usually the case, and not separable into definite longitudinal and circular bands, and internal to this a single layer of cells set on a basement membrane. The cells are of the same kind as those observed in the lower part of the mid-gut of *Philaematomyia* and other Muscids. They are cubical or columnar, and present a most irregular picture in most sections, many of the cells being in the act of discharging their secretion into the lumen of the gut, while others have emptied themselves and are degenerating. In many of the cells the nucleus is situated near the lumen, and the portion of the cell containing it is connected with the remainder only by a narrow neck. In other parts fairly regular rows of cubical cells, with granules and some vacuoles in their substance, may be found. Blood at all stages of digestion is seen in fleas dissected immediately after removal from the host.

The *hind-gut* is narrow, and is rather shorter than the mid-gut. It lies curled up in the posterior part of the abdomen, and dilates distally to form a pear-shaped rectum, in which there are six rectal papillae similar to those of the Diptera. There are four Malpighian tubes, which enter the gut at the posterior end of the stomach by separate openings.

The salivary glands

There are two pairs of *salivary glands* (Plate LVIII, fig. 11) on each side, each two giving off fine ducts which unite after a short course to form a common duct, the common ducts of the two sides uniting in the neck and passing to the salivary receptacle just behind the hypopharynx. Each gland is rounded or slightly oval, with the narrow end directed forward, and is composed of a single layer of comparatively large cells arranged around a central lumen. The common duct on each side and the distal portion of the duct of each gland are provided with the familiar arrangement of chitinous rings to prevent the collapse of the tube when the saliva is drawn forwards by suction.

PLATE LVIII

Figure 1. The thoracic and abdominal chain of nerve ganglia of *Ctenocephalus felis.* ×66.

Figure 2. The second and third abdominal ganglia, more highly magnified. Note the separation into two bilateral halves, and the commissure connecting the two ganglia.

Figure 3. The alimentary tract of *Ctenocephalus felis.*

Figure 4. One of the chitinous spines from the proventriculus, isolated.

Figure 5. An undeveloped ovarian tube. Such masses of cells are to be found in fleas which also possess mature ovarian tubes.

Figure 6. The male organs of reproduction of *Ctenocephalus felis.*

Figure 7. An ovarian tube, the last egg of which is nearly mature.

Figure 8. A portion of a cross-section through the proventriculus, showing the chitinous rods running towards the centre of the cavity. Each turns backwards in the long axis.

Figure 9. A transverse section through the proboscis, near the upper end, showing the food channel, f.c., formed by the mandibles and epipharynx, and the salivary groove.

Figure 10. A transverse section through the base of the proboscis.

Figure 11. The salivary glands of *Ctenocephalus felis.* Note that there is a pair on each side.

Figure 12. The distal portion of the salivary duct, entering the gland.

PLATE LVIII.

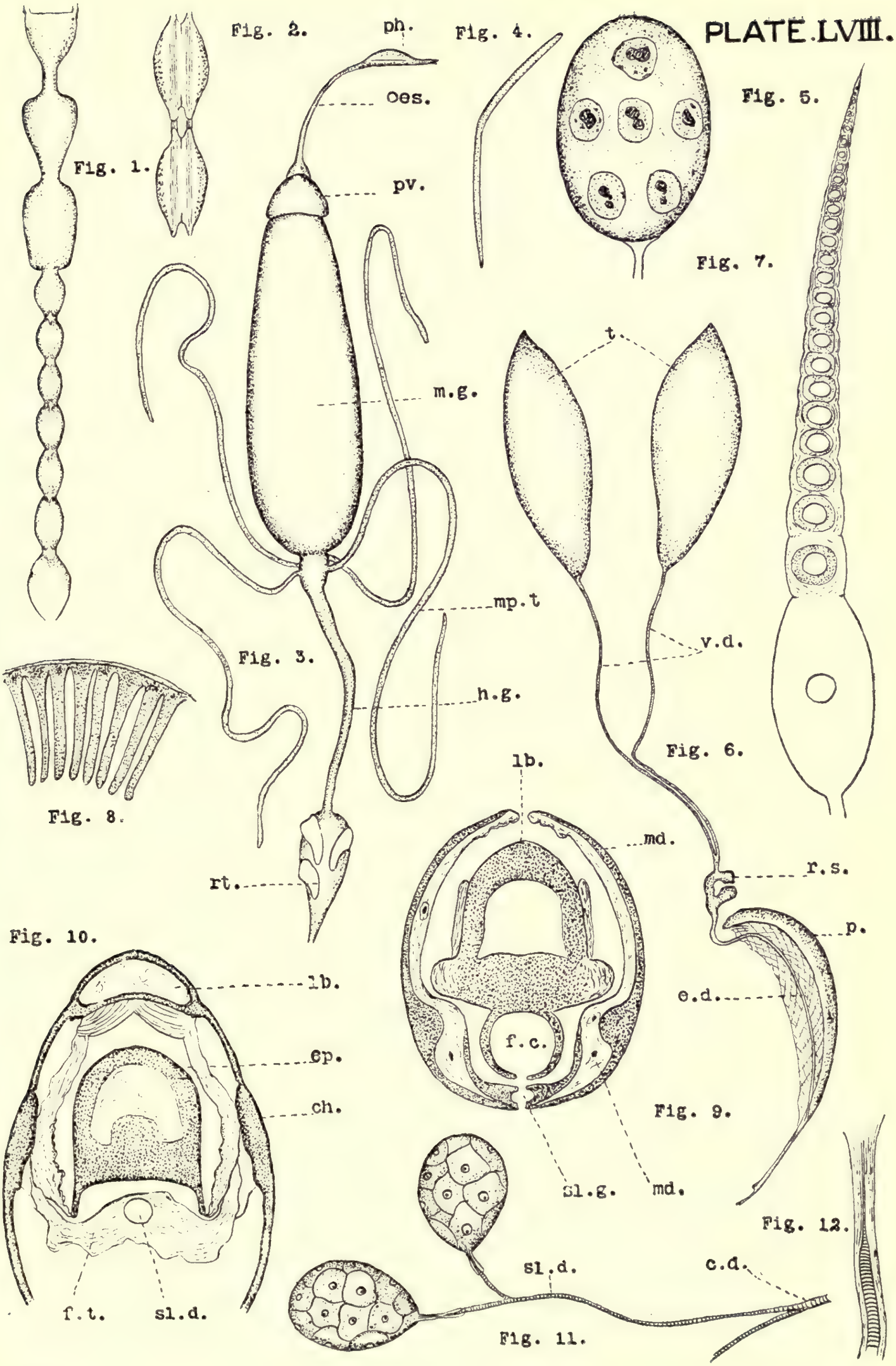
Fig. 1.
Fig. 2.
ph.
oes.
pv.
m.g.
mp.t
Fig. 3.
h.g.
rt.
Fig. 4.
Fig. 5.
Fig. 7.
t.
v.d.
Fig. 6.
r.s.
p.
e.d.
Fig. 8.
lb.
md.
f.c.
Fig. 9.
sl.g.
md.
Fig. 10.
lb.
ep.
ch.
f.t.
sl.d.
Fig. 11.
sl.d.
c.d.
Fig. 12.

The *salivary pump* lies below the anterior portion of the pharynx, and consists of a small chitinous chamber, to the walls of which there is attached a series of dilator muscles. These presumably act in the same way as those of the salivary pump in other insects, drawing the walls of the pump apart so as to suck up the saliva from the glands by means of the induced negative pressure.

The reproductive system. The male organs

The male organs of reproduction (Plate LVIII, fig. 6) consist of a pair of rather large *testes*, spindle-shaped and pointed at both ends, an extremely fine efferent duct from each, and a complex penis. The posterior portions of the *vasa differentia* are enclosed in a common sheath of fibrous and muscular tissue, so that there appears to be a common duct, but examination of suitably stained preparations shows that the two ducts do not unite until they reach the base of the penis sheath. At this point there is a small pouch of an irregular shape, consisting of two horizontal limbs united by a vertical one. The two ducts from the testes open into this seminal receptacle by a common opening, while the common ejaculatory duct leaves its posterior side at the angle between the posterior transverse limb and the vertical one. The penis and its sheath together constitute an extremely complex sexual organ. The *penis* or central portion is a curved rod, bent upwards and backwards, and hollowed on its upper concave side, where the concavity is filled in by a sheet of membraneous tissue, in which the course of the ejaculatory duct can be traced. It terminates in a flat open gutter of extreme fineness. The sheath around this consists of a plate of chitin bent in the same direction, and concave on its upper surface, partly enclosing the penis. To this are attached several curved rods on each side, which appear to act as apodemes in the mechanism of extrusion of the penis in copulation. The whole apparatus is composed of chitin as thick as that of the exoskeleton, so that it becomes conspicuous in cleared preparations, and enables one to distinguish the sex at a glance.

Female organs of reproduction

The organs of the female are the ovaries, ovarian ducts, and the spermatheca. The *ovaries* consist of eight ovarian tubes on each side. leading to a short common duct which opens just ventral to the anus. The *spermatheca* is a small U-shaped chitinous pouch, which, like the male sexual organ, becomes conspicuous when the soft tissues are dissolved out of the body of the flea. The shape and size of the pouch vary in different species, and are sometimes used as points of distinction. The writers have never succeeded in dissecting out the duct which leads from the spermatheca to the oviduct.

The ovaries are of a different type to those of the Diptera. Each ovariole, (Plate LVIII, fig. 7) when mature, consists of a long tube which tapers gradually from base to apex. The lower portion is divided into a series of follicles, three or four being generally distinguishable. Of these the lowest contains a mature egg, while the next two or three contain nurse cells and ova of approximately the same size as one another. The rest of the tube is filled up with a large number of young ova, diminishing in size and degree of maturation from the base upwards in a gradual manner. The lowest seven to ten of these are slightly less in width than the tube in which they lie, and are partially separated from one another at the sides, though the marginal epithelium is not developed. Higher up the ova are smaller and are more crowded together, two often lying side by side in the transverse axis of the tube, and higher still they diminish rapidly in size until they form a crowded mass of cells at the upper part of the tube. As many as twenty ova can be distinguished in some of the ovarioles.

All the ovarian tubes in the same flea are not in the same degree of development, and even when the abdomen is obviously distended and the flea about to oviposit one finds some of the ovarian tubes in an immature condition. In many fleas, even in those which have some ova almost mature, one finds ovarian tubes which are almost entirely undifferentiated, consisting only of a mass of large cells (Plate LVIII, fig. 5) attached to the oviduct by a fine canal. Probably only a small number of eggs is deposited at one time, oviposition being repeated a large number of times at short intervals.

The *respiratory system* is simple, each spiracle giving off a trachea which breaks up at once into a number of branches for the supply of the adjacent tissues. There are no air sacs.

The nervous system

The *nervous system* (Plate LVIII, fig. 1) shows a remarkably low degree of differentiation. The brain consists of two lateral masses, corresponding to the supra-oesophageal ganglia, which are united to one another by a broad commissure, and two almost equally large ganglia below and behind them, the sub-oesophageal ganglia; the two pairs of ganglia are united by commissures which enclose the oesophagus. The three thoracic ganglia are distinct from one another and are of approximately equal size. There are seven abdominal ganglia, all equal in size except the last, which is larger than the rest. Both the thoracic and abdominal ganglia show evidence of being composed of two lateral halves. This primitive condition of the nervous system is a strong argument against fleas having had winged ancestors. They are not degraded Diptera.

DISSECTION

While it is a matter of very great difficulty to make a complete dissection of any of the systems of the flea, it is comparatively easy to get out any one organ for examination. The one point which it is absolutely essential to attend to before one can have any hope of success is to see that the needles are sharp. The integument of the flea is a very tough one, and some parts of it are extremely hard to cut steadily. Before commencing the dissection the legs should be cut off or pulled off near the body, if possible tearing out the coxae.

Dissection of the mid-gut

The mid-gut may be obtained by the following method. Place a blunt needle firmly on the thorax, holding it rather flat. If the flea cannot be steadied in this way insert the point of the needle between the head and the prothorax, just at or behind the pronotal comb if there is one. Keeping this needle steady, place the other, which should be very sharp, on the first segment of the abdomen, and press it slowly down towards the slide. The point will not at first pierce the integument, but will slip to one side, and by gradually increasing the pressure as the margin is approached one can nip a piece of either the dorsal or the ventral margin between the point and the glass. It is best to take the dorsal margin. Now pull gently, keeping a firm grip with both needles. The abdominal tergite will then separate from its attachment to the metathorax at the dorsal angle. When once the separation has begun it can be increased by putting both needles in the fissure and widening it. Next *cut* the last segment of the abdomen away from the body with a sharp blade-like needle, so as to loosen the posterior attachment of the gut. When this has been done place one needle on the last remaining segment and one on the head or prothorax, and pull gently. The proventriculus and mid-gut will come out of the abdomen and will remain attached to the head by means of the fine oesophagus. They can then be easily separated and removed to another slide.

The hind-gut

The hind-gut is comparatively easy to remove; it lies coiled up at the posterior end of the body, so that one can safely begin by cutting across the anterior portion of the abdomen, probably severing the mid-gut. Then by stroking the remaining portion gently with a needle from behind forward the ovaries and a good deal of the fat body can be made to extrude at the anterior opening, and can be torn out. Having reduced the contents of the abdomen in this way, insert the point of a sharp needle between the dorsal margins of the eighth and ninth segments, and pull backwards, steadying the remainder by a needle held on the anterior portion of the ventral margin. The last segments can in this way be torn out with the rectum and hind-gut still attached.

Salivary glands

To dissect out the salivary glands, place a rather blunt needle in the antennal pit, piercing the head if necessary to get a good hold. Then insert a needle bent like a retractor in the space between the metanotum and the first abdominal tergite, and pull the two apart by steady traction. The salivary glands will float out in the saline as the segments are drawn away from one another, and can be recognized by their glistening appearance.

The Ovaries

Mature ova are very easily obtained by making a slit in the abdominal wall and compressing the body, when they are forced out. It is as well to do this in all dissections, even if they are not required, as it leaves one more room to work. If the complete organ is required the only way to obtain it is to patiently chip away all the tergites or sternites at the dorsal or ventral margin. It should be remembered that the apical filaments of the ovaries are attached in the dorsal and anterior part of the abdomen, and an effort should be made to avoid tearing these attachments till the rest of the organ is free, or they will spread out all over the slide.

COLLECTION AND PRESERVATION OF SPECIMENS

Fleas can be most readily obtained from the animals on which they feed, though failing this one can usually obtain them, either as larvae or pupae, from the nests of the host. The latter is the most convenient source in the case of the bird fleas.

It is important to remember that all fleas will leave the body of the host immediately it dies, and that therefore one has to be very quick in collecting them from an animal which has been killed. With small mammals captured alive it is generally easy, when they are plentiful, to pick them off with a pair of forceps, or, if they are very small, with a stiff brush moistened with water. A comb with fine teeth is also very useful. Fleas are often confined to some particular part of the host's skin, such as the rump, or the lower part of the abdomen, and a careful search should be made before deciding that they are absent. In the case of the more active fleas, and when there are only a few on each animal, the host should be chloroformed, as this makes the fleas come out of the hair and renders them sluggish in their movements. It does not as a rule kill them, even if the host is killed, and they soon become sufficiently active to escape if not caught.

The nests of birds and mammals suspected to harbour fleas should be brought to the laboratory entire, securely tied up in a cloth bag. The contents are then spread out bit by bit on a large sheet of white paper, and examined with a hand lens for larvae and pupae. The larvae, and the imagines if present, are easily recognized by their movements when the eye becomes accustomed to them.

Fleas should be preserved in alcohol, or, what is better, mounted at once. This is done by clearing them in caustic potash and mounting on slides in canada balsam. If fixed in alcohol first and subsequently cleared for mounting the chitin is apt to become too much decolourized and too transparent before the hardened internal organs are dissolved out. Care should be taken in mounting them to spread out the legs so that one of each pair can be seen distinctly. It is frequently necessary, in order to identify the species with certainty, to dissect off the external genitalia and mount them separately, and in doing this, as in all other manipulations with fleas, the greatest care must be taken not to damage the bristles, which are of so much importance in identification.

When sending fleas to experts for identification some at least should be sent in alcohol. It is essential to give the host's name and locality.

Fleas for identification may be sent to

The Hon'ble N. C. Rothschild,
Arundel House,
Kensington Palace Gardens,
London, W.

or to

Mr. Carl Baker,
United States National Museum,
Washington, U.S.A.

LITERATURE

Baker, C. F. ... A Revision of American Siphonaptera, or Fleas, together with a complete list and bibliography of the group. *Proceedings of the United States National Museum,* Vol. xxvii, pp. 365—469, Washington 1904.

BAKER, C. F.	The Classification of the American Siphonaptera. *Proceedings of the United States National Museum*, Vol. xxix, pp. 121–170. 1905. The first paper contains a systematic account of the American genera and species of fleas, including descriptions of many new species. The second paper is supplementary to the first.
HARMS, BRUNO.	Untersuchungen über die Larve von *Ctenocephalus canis*, Curtis. I. Teil. 13 Text Figures and one Plate. *Archiv für Microskopische Anatomie*. Band 80. Heft 2, 1912. This paper contains a well illustrated description of the internal anatomy of the larva of *Ctenocephalus canis*.
JORDAN, K. and ROTHSCHILD, N. C.	A Revision of the Sarcopsyllidae, a family of the Siphonaptera. *Thompson Yates and Johnston Laboratories Reports*, Vol. vii, Part i, 1906. An account of the Sarcopsyllidae; morphology, classification, descriptions of new species; fifty-six pages with four plates and a full bibliography.
Idem	Revision of the non-combed eyed Siphonaptera. *Parasitology*, Vol. i, No. 1, 1908. Ninety-nine pages, seven plates, full bibliography. This paper deals very fully with the group of genera allied to and including *Xenopsylla*.
Reports on Plague Investigations in India.	Published as supplementary numbers to the *Journal of Hygiene*, Vol. vi to xii, 1906 to 1912. These reports contain a large number of papers dealing with the rat flea and its allies in relation to the transmission of plague, including many important observations on bionomics, breeding habits and technique. Among them may be noted the following:— September, 1906. The Physiological Anatomy of the Mouth Parts and Alimentary Canal of the Indian rat flea, *Pulex cheopis*. July, 1907. On the External Anatomy of the Indian rat flea, *Pulex cheopis*, and its differentiation from some other common fleas. (The description of the external anatomy is not in accord with the views of Jordan and Rothschild in some particulars.) December, 1912. Observations on flea-breeding in Poona. The special cages which were used in the demonstration of the passage of plague from rat to rat by means of the flea are described and figured in the first supplement, September, 1906.
ROTHSCHILD, N. C.	Notes on *Pulex canis* and *felis*. *Ent. Rec. and Journ. of Var.*, Vol. xiii, p. 126, 1901.
Idem	Some further notes on *Pulex canis*, Curtis and *Pulex felis*, Bouché. *Novit. Zoolog.*, Vol. xii, pp. 192–3 1905. These two papers give the diagnostic points between the two species.

ROTHSCHILD, N. C. A Synopsis of the Fleas found on *Mus norwegicus decumanus*; *Mus rattus alexandrinus*; and *Mus musculus*. *Bulletin of Entomological Research*, Vol. i, July, 1910.

Rothschild has published a large number of papers, dealing mainly with new species and genera, in *Novitates Zoologicae*, *The Entomologist's Monthly Magazine*, *Entomologist*, *Entomologist's Record and Journal of Variations*, etc. Complete lists of references to the older literature on the Siphonaptera will be found in the papers of Baker, Jordan and Rothschild, quoted above. There are a few references in the Reports of the Plague Commission.

CHAPTER VI

THE ORDER RHYNCHOTA: BUGS

THE order Rhynchota comprises a large and very varied group of insects, all the members of which are armed with a jointed, suctorial proboscis which is flexed under the head. Many of the aquatic forms, such as the water boatmen, pond skaters and water scorpions, are familiar natural history objects and may be seen in almost any collection of water. Another aquatic species, which is often mistaken for a beetle, is the well-known *Belostoma*, the largest of all bugs; at certain seasons *Belostoma indica*, the common Indian species, is often caught in large numbers round any lighthouse, and *B. Deyrollei* around the search lights of river steamers in parts of Assam. Among the terrestrial forms the Cicadas are familiar insects in all the hill stations of India, where their shed skins may be found attached to the barks of trees; the shrill notes of the male *Cicada* are well known. Many of the smaller terrestrial bugs are abundant during the rainy season in the tropics, and often come into houses at night. Others may be seen in swarms feeding on the juices of plants; as many of these are brightly coloured insects, they are very attractive objects.

Although the majority of bugs are plant feeders, quite a number are predaceous. The well-known pond skater *(Gerris)* is a good example of a predaceous bug; it is often seen resting on the surface of water in a well or tank with some insect, often one of its own kind, impaled on its proboscis.

The order Rhynchota is of considerable economic importance, for many of the species are among the most serious pests which the agriculturist has to contend with. The species belonging to the genera *Oxycarenus* and *Dysdercus* cause much damage to cotton in many parts of the world. *O. hyalinipennis*, the Egyptian cotton stainer, punctures the cotton bolls with its proboscis and also stains the fibre with its excrement. Tea, coffee, and garden produce of all kinds, are similarly attacked by various species of bugs.

On the other hand a few bugs are of use to man. The well-known lac, a commercial product, is obtained from a species of coccid; the Cochineal bug, *Coccus cacti*, yields the familiar dye.

At present very little is known regarding the habits and life histories of the Rhynchota, and there is, therefore, a wide field for research in this direction. With regard to their affinities to other insects no two entomologists are agreed, so that mere statements of the views which are held would be of little practical use.

Bugs are of considerable interest to the parasitologist, as many of the commonest species are infected with various kinds of protozoal parasites, of which the flagellates of the genera *Herpetomonas* and *Crithidia* are the best known. One of these parasites, *H. lygaei*, Patton, from *Lygaeus pandarus*, is indistinguishable in its pre and post-flagellate stages from the parasite of Kala Azar as seen in man. According to Lafont the flagellate parasitic in *Conorhinus rubrofasciatus* in Mauritius, if inoculated intraperitoneally into mice, becomes transformed into a trypanosome in the blood.

The blood-sucking bugs are confined to the families Reduviidae and Cimicidae, and only about a dozen species are known to have this habit, the bed bugs, *Cimex lectularius* and *C. rotundatus*, being the most familiar. The family Polyctenidae contains a few very aberrant bugs which are parasitic on bats; very little is known regarding them.

Blood-sucking Bugs in relation to Disease

Of all the blood-sucking insects associated with man, the bed bug is unquestionably the commonest; although its sanguivorous habits are well known, yet from the point of view of disease it is the least understood of all human pests. In reviewing the 600 odd papers dealing with *Cimex lectularius*, Girault points out that those who have studied it from the entomological standpoint exhibit an entire lack of knowledge of the medical literature connected with it; the medical man, on the other hand who, discusses this insect from the disease standpoint, shows an equal deficiency in his knowledge of the entomological literature relating to it, and more particularly of that dealing with its structure.

In 1887 Metchnikoff, in a paper on Relapsing Fever, referred to the rôle of the bed bug, *Cimex lectularius*, in disease; this is the first time that this insect is definitely suspected. Since then numerous attempts have been made to associate it with the transmission of various kinds of pathogenic bacteria, particularly the bacillus of plague. Verjbitski, however, is the only observer who has brought forward any substantial experimental proof that *lectularius* can transmit *Bacillus pestis*.

Goodhue and others have endeavoured to demonstrate that *lectularius* may also carry the bacillus of leprosy; the evidence which has been brought forward in support of this hypothesis is, however, far from convincing.

The senior author, as the result of feeding experiments, has shown that the parasites of Kala Azar and Oriental Sore undergo their flagellate stages in the mid-gut of the Indian bed bug, *Cimex rotundatus*. Owing to the difficulty of obtaining a highly susceptible animal it has not yet been possible to transmit these parasites by the bite of this bug. The evidence that it carries these parasites in nature is, therefore, based on the study of the development of the parasites in its mid-gut, and on the fact that they do not develop into flagellates in any other blood-sucking arthropod experimented with.

Chagas has recently shown that a large reduviid bug, *Conorhinus megistus*, is the invertebrate host of a human trypanosome, *T. cruzi*, in parts of Brazil. There are several close allies of this bug in North and South America, and at least one in the Oriental Region.

EXTERNAL ANATOMY

Before dealing with the classification of the Rhynchota and the descriptions of the various important species, it will be convenient to give a short general account of the external structure, such as that of any common reduviid. As the species belonging to the genus *Cimex* are somewhat aberrant the external anatomy of *Cimex rotundatus* will be discussed separately.

The head

The body of a bug is distinctly divided into head, thorax and abdomen. The *head* exhibits great variation in shape and in the manner in which it is attached to the thorax. In many species of the Homoptera it is situated on the under surface and its distal edge is directed backwards. In the Heteroptera the head is often small and inconspicuous as compared with the rest of the body of the insect. In some pentatomids it is broadly expanded and armed with lateral horns; in many reduviids on the other hand the head is narrow and elongated. The antennae as a rule consist of four or five joints, which are nearly always long and slender. In *Belostoma* the antennae are concealed in pits on the under surface of the head, and have several branched processes; in many coreids the segments are broadly expanded. The eyes of bugs are usually situated laterally and are generally prominent structures; there are either two or three ocelli situated behind the eyes.

The *thorax* consists almost entirely of the *prothorax*, which forms a large conspicuous plate of chitin, often with sharp lateral angles;

it may be brightly coloured, and in many of the species of Homoptera is prolonged backwards over the abdomen in the form of a horn. The *meso-* and *metathorax* are concealed under the scutellum and elytra, and can only be seen by dissecting off these parts; their shape and size varies in the different species. The *scutellum* is nearly always well developed; it may be prolonged into a sharp point or produced into a broad process, when it conceals the wings.

The Abdomen

The exact number of abdominal segments is still a matter of dispute, but as a rule eight can be clearly distinguished. In many of the Heteroptera, particularly among the species of the family Reduviidae, the lateral abdominal margins are greatly developed, forming a plate-like expansion which is known as the *connexivum*. In the genus *Conorhinus* this is well developed and is especially conspicuous when the bug is in a starving condition; most of the species have coloured spots and stripes on the connexivum, which are used as taxonomic characters (Plate LIX).

The females in many species of the Heteroptera have relatively long pointed ovipositors; the external genitalia of the males are often very conspicuous and have large claw-like claspers. During copulation the sexes usually become firmly attached to each other, remaining so for a considerable time.

Stink glands

As is well-known most bugs emit strong offensive odours. The stink glands of the adults are as a rule situated at the base of the abdomen, the ducts opening by means of an orifice on each side of the metasternum. In the larvae and nymphs the stink glands are situated on the dorsal surface of the abdomen and open by ducts on each side of the mid-dorsal line. As a rule the plant feeding Heteroptera have stink glands, while many of the predaceous species are without them.

Wings

The wings of bugs exhibit great diversity of form. There are two pairs, the anterior of which are known as the *elytra*, *hemielytra* or *tegmina*. Each hemielytron consists of a basal horny portion and a membraneous apical part. In the Heteroptera the basal part is divided into several distinct portions separated by ridges. The *corium* (Plate LXII, fig. 8) forms the largest part of the basal portion. Internal to it, and next to the scutellum in the folded condition of the wing, is the *clavus*, which is often sharply demarcated from the corium by a distinct ridge; the outer and costal part of the wing is called the *embolium*. In the family Capsidae the apical part of the corium is separated off from the rest and is then termed the *cuneus.* The second or hind pair of wings are entirely membraneous.

The legs are well developed and consist of coxae, femora, tibiae and tarsi. In many of the species of Heteroptera the hind tibiae are furnished with peculiar leaf-like expansions. The tarsus is usually three-jointed and armed with a pair of claws.

CLASSIFICATION

Up to a certain point the grouping of the Rhynchota into families and subfamilies is agreed upon by most authorities, but the arrangement of the numerous genera and species, and their relations to each other, are still matters of dispute. The following classification is taken from Distant's work on the Indian Rhynchota in *The Fauna of British India,* Vols. I to V.

Distant divides the Rhynchota into two suborders as follows:—

Front of head not touching the coxae	Suborder	**Heteroptera**
Front of head much inflexed so as to be in contact with the coxae	Suborder	**Homoptera**

The Heteroptera are divided into two series as follows:—

Bugs with conspicuous antennae, capable of being moved freely in front of the head	Series	**Gymnocerata**
Bugs with their antennae concealed, either situated on the underside of the head, to which they are closely pressed, or in foveae under the head (aquatic)	Series	**Cryptocerata**

The series Gymnocerata contains all the terrestrial Heteroptera, and a few families which live on the surface of water or in damp mud; the Cryptocerata includes all those forms which live under water.

Distant gives the following Key to the families of the Gymnocerata:—

1.	Abdomen not clothed with a silvery velvety pubescence (species not aquatic).	**2**
	Abdomen clothed beneath with a silvery velvety pubescence (species aquatic or sub-aquatic)	**16**
2.	Scutellum reaching at least to the base of the membrane, or at least half as long as the abdomen, sometimes covering the whole of the abdomen above and the anal appendages .	**Pentatomidae.**
	Scutellum not reaching to the base of the membrane, nor to the middle of the abdomen	**3**
3.	Mesopleurae and metapleurae composed of one piece only; hemielytron without a cuneus	**4**
	Mesopleurae and metapleurae composed of several pieces; hemielytron with a cuneus	**13**
4.	Tarsi three-jointed	**5**
	Tarsi two-jointed	**11**
5.	Rostrum not bent at base, lying in repose against the under surface of the head	**6**

	Rostrum stout, bent at base so that it does not lie against the under surface of the head	9
6.	Antennae generally elongate, and four-jointed, inserted on the upper parts of the sides of the head	7
	Antennae inserted below a line drawn from the course of the eye to the apex of the face	8
7.	Legs of moderate length, apices of femora not nodulosely clavate	**Coreidae.**
	Legs long and slender, apices of femora nodulosely clavate	**Berytidae.**
8.	Ocelli present	**Lygaeidae.**
	Ocelli absent	**Pyrrhocoridae.**
9.	Rostrum long, ocelli placed between the eyes	**Saldidae.**
	Rostrum short, ocelli when present placed behind the eyes	10
10.	Hemielytra complete, membrane distinct	**Reduviidae.**
	Hemielytra entirely membraneous	**Heniocephalidae.**
11.	Anterior legs normal	12
	Anterior legs short and stout, with long coxae, short thick femora, and curvate pointed tibiae, frequently without tarsi	**Phymatidae.**
12.	Hemielytra more or less reticulate, consisting of strong irregular thick lines, forming a framework of cells. Anterior legs inserted on the posterior margin of the prosternum	**Tingididae.**
	Hemielytra neither reticulate nor cellular, anterior legs inserted on the disc of the prosternum	**Aradidae.**
13.	Hemielytron with an embolium	14
	Hemielytron without an embolium	**Capsidae.**
14.	Ocelli absent	**Cimicidae.**
	Ocelli present	15
15.	Antennae long and thin, clothed with long hairs, third and fourth joints together twice as long as first and second	**Ceratocombidae.**
	Antennae not very thin, nor clothed with long hairs, third and fourth joints not nearly as long as first and second	**Anthocoridae.**
16.	Antennae five-jointed	**Hebridae.**
	Antennae four-jointed	**Hydrometridae.**

The two families Aëpophilidae and Polyctenidae are not included in the above key; the former are of no practical importance. The genus *Polyctenes* contains a few species which are parasitic on bats.

Distant gives the following Key to the families of the Cryptocerata:—

1.	Body short and broad; head very broad with prominent eyes; ocelli present. Posterior legs thin, formed for running	**Pelogonidae.**
	Body elongate or ovate; head of moderate size	2
2.	Anterior legs inserted on disc of anterior margin of prosternum	3
	Anterior legs inserted on the posterior margin of prosternum	5
3.	Antennae with four joints; no anal appendage	4
	Antennae with three joints, abdomen with a long tubular appendix	**Napidae.**
4.	Posterior tibiae spinulose	**Naucoradidae.**
	Posterior tibiae flattened and provided with swimming hairs.	**Belostomatidae.**
5.	Rostrum free, three to four-jointed	**Notonectidae.**
	Rostrum concealed, apparently unjointed	**Corixidae.**

Before describing the blood-sucking species short reference will be made to those bugs which are of interest to the parasitologist.

FAMILY PENTATOMIDAE.

This family, which is the largest of the Heteroptera, is usually divided into fourteen subfamilies, each of which contains many genera and species. Most pentatomids are remarkable for their beautiful colouration, especially the species which belong to the subfamily Scutelleraria; those of the subfamily Tessaratominae, although usually of more sombre colours, are often of considerable size. *T. javanica*, the bug found on the soap-nut tree, is a large insect common in many parts of India. It possesses large stink glands, secreting a strong smelling fluid, which it can eject to a distance of several inches. The subfamily Pentatominiae contains among others two species, *Erthesina fullo* and *Halys dentatus*, which are naturally infected with flagellates, the former with a species of herpetomonas and the latter with a crithidia. The flagellate of *Halys dentatus* is another good example of a typical crithidia which is parasitic in an insect which does not suck blood.

FAMILY LYGAEIDAE

The bugs belonging to this family are of great economic importance, as many of the species are very destructive to food plants. Lygaeids are chiefly distinguished from coreids, to which they are closely allied, by their antennae, which are inserted on the side of the head, and also by the presence of ocelli. Most of the species are small, but they are as a rule very active, and readily take to flight if an attempt is made to catch them.

Several of the species belonging to this family are infected with flagellates. *Oxycarenus laetus*, which is common on the cotton plant in Madras, is nearly always infected with a species of *Herpetomonas*. This bug lays its eggs near the cotton seeds and all the stages may be found collected together in the boll, feeding on the juice of the seeds. *Lygaeus pandarus* (*militaris*), another lygaeid which is common on the milk plant, *Calotropis gigantea*, is nearly always infected with *Herpetomonas lygaei*, a flagellate which very closely resembles the parasite of Kala Azar. *Lygaeus hospes* is infected with the same parasite. *Nysius minor*, a small bug which lives on the latex juice of the common weed *Euphorbia pilulifera* in India, is of peculiar interest, for it is in all probability the invertebrate host of *Herpetomonas davidi*, which is parasitic in the milky juice of the plant; according to Lafont an allied species of *Nysius* is the host of the same parasite in the Island of Reunion. Robertson has recently recorded a herpetomonas and a crithidia from the alimentary tract of *Dysdercus casiatus*, the red cotton bug of Uganda, which has never been known to suck blood.

FAMILY COREIDAE

This family of bugs is a comparatively small one; many of the members have extraordinary dilatations on their antennae and tibiae, the function of which is unknown. The antennae are inserted on the upper side of the head, above a line drawn from the eyes to the base of the proboscis. Robertson records a herpetomonas from the alimentary tract of *Leptoglossus membranaceus* in Uganda; the parasite was found to invade the salivary glands. She considers it a good example of 'the 'independent development in a sucking insect of all the factors requisite 'for the transmission of a flagellate, parasitic in the intestine, by way of 'the mouth parts of the insect host'. There is no record that this bug sucks blood; it is entirely a plant feeder.

BLOOD-SUCKING BUGS

FAMILY REDUVIIDAE

Head more or less elongate and freely moveable; ocelli may or may not be present; if present they are situated behind the eyes. Proboscis moderately short and stout and does not lie in repose in a groove on the under surface of the thorax, but is looped under the head. The prothorax is well developed. The wings in repose lie close up against the abdomen. Elytra when present consist of three divisions. Tarsi three-jointed. (Distant).

Many of the species of the Reduviidae are predaceous and feed on the body juices of other insects; the majority, however, are plant feeders. As a rule they are diurnal in their habits, but some are entirely nocturnal, and often fly into houses at night; they should be handled with care, as they are capable of inflicting a painful bite. Several of the species which are met with in the field in their larval and nymphal stages protect themselves in a peculiar manner. They are most frequently encountered at the openings of holes in the ground; the observer who sees them for the first time may be under the impression that he has discovered some new form of insect life, for the larva and nymph cover their bodies with particles of sand, small pieces of stick, dust and other debris until they are completely hidden. If one is caught in the fingers the debris surrounding it comes off and its true nature is revealed. In Madras the nests of mound-building termites are favourite places for the early stages of a species of *Acanthaspis*.

The Reduviidae are of the greatest interest to the medical man, as it is in this family that the large blood-sucking species are to be found. Darwin was the first to record the blood-sucking habit of a South American reduviid, *Conorhinus infestans*, Klug; it is interesting to note what he says about it in his *Journal of a Naturalist*. 'We slept in the 'village of Luxan, which is a small place surrounded by gardens and 'forms the most southern cultivated district in the Province of Mendoza; 'it is five leagues south of the capital. At night I experienced an attack '(for it deserves no less a name) of the Benchuca, a species of *Reduvius*, 'the great black-bug of the Pampas. It is most disgusting to feel soft, 'wingless insects about an inch long crawling over one's body. Before 'sucking they are quite thin, but afterwards they become round and 'bloated with blood, and in this stage are easily crushed. One which 'I caught at Iquique (for they are found in Chili and Peru) was very 'empty. When placed on a table and though surrounded by people, if a 'finger was presented, the bold insect would immediately protrude its 'sucker, make a charge and, if allowed, draw blood. No pain was 'caused by the wound. It was curious to watch its body during the act 'of sucking, as in less than ten minutes it changed from being as flat as 'a wafer to a globular form. This one feast for which the benchuca 'was indebted to one of the officers, kept it fat during four months; but 'after the first fortnight it was ready to have another suck'.

The blood-sucking reduviid which has attracted the most attention is *Conorhinus megistus*, Burm. This species is the invertebrate host of *T. cruzi*, which causes a fatal form of human typanosomiasis in many parts of Brazil. As far as is known at present all the blood-sucking reduviids belong to the genus *Conorhinus*. According to Distant this genus belongs to the sub-family Acanthaspidinae, and is placed in the division Conorhinaria.

DIVISION CONORHINARIA

Head long, porrect; anteocular portion of head longer, generally very much longer, than postocular; a more or less distinct transverse impression between them or immediately between the eyes. (Distant).

PLATE LIX

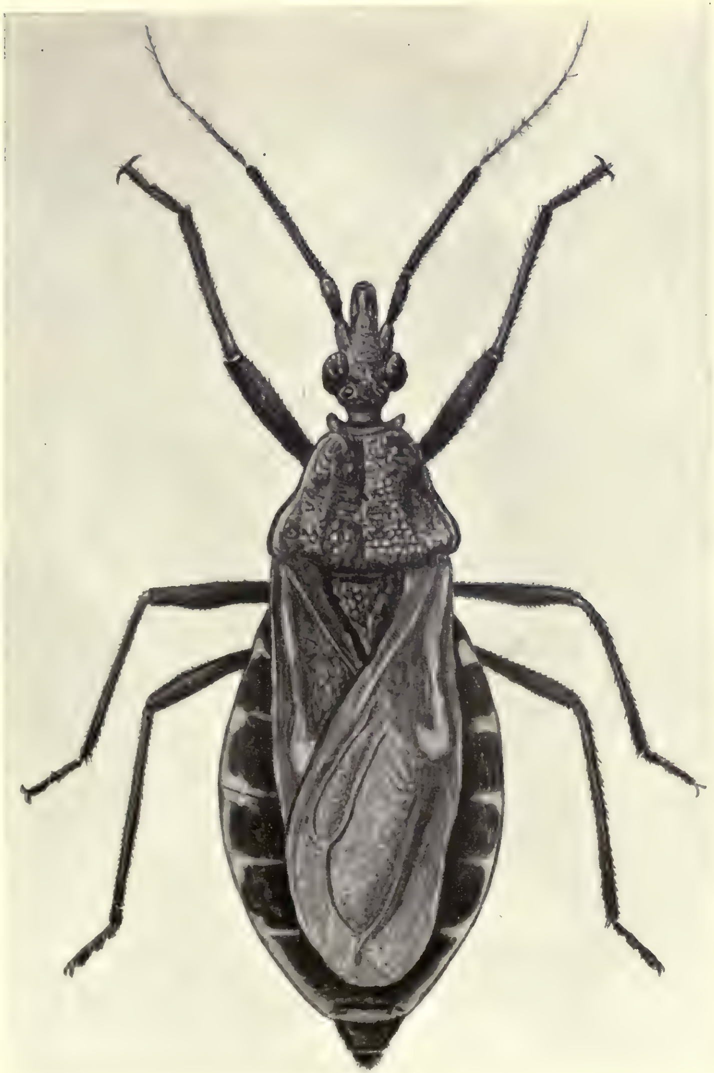

Fig. 1. Conorhinus rubrofasciatus, ♀. × 5.

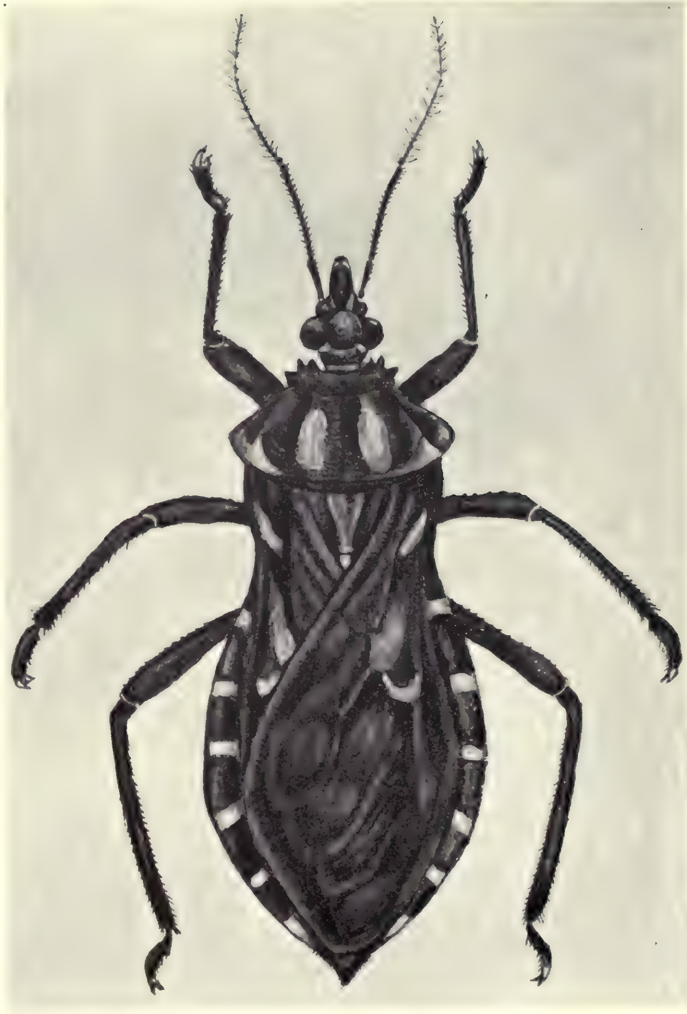

Fig. 2. Conorhinus megistus, ♀. × 4.

According to Distant this division contains four genera, only one of which, *Conorhinus*, concerns us here.

GENUS CONORHINUS, LAPORTE.*

Head long, porrect, more or less distinctly impressed behind the eyes; rostrum with the first joint very much shorter than the second; antennae inserted on the sides of the head about midway between eyes and apex; ocelli placed very far apart; prosternum broadly sulcated; abdomen strongly ampliated, not centrally carinate, frequently with the disc prominently flattened; posterior tibiae longer than the femora. (Distant).

The bugs belonging to this genus are of considerable size, often measuring an inch or more in length. All the species are of a dark brown to black colour, with reddish or yellowish lines and spots on the head, thorax, wings and connexivum. The male can be distinguished from the female by the shape of the end of the abdomen; in the male it is rounded off, while in the female it is pointed; the male hypopygium is well developed and forms a prominent swelling on the ventral surface. The eyes are very prominent and form two lateral rounded swellings; the ocelli, which are behind and above the eyes, are well developed, and often appear as clear spots. The proboscis is short and stout and is held in a looped manner under the head.

The species are widely distributed and are found in the Neartic, Neotropical and Oriental regions.

Conorhinus rubrofasciatus, de Geer. (Plate LIX, fig. 1.) Pisceous brown. Head dark brown to black with the basal margin reddish. Antenna, first joint not quite reaching apex of head; second joint three times the length of first; the basal joints dark, apical joints light. Pronotum dark brown to black; anterior angles produced into two short spines of a reddish yellow colour. Two blunt prominences ending in diverging ridges on anterior portion of dorsal surface of pronotum; lateral margin of pronotum to posterior angles with a reddish yellow linear streak; scutellum dark, apex occasionally reddish; corium with a basal oblique linear streak and a somewhat diffuse subapical reddish yellow spot; wing membrane fuscous. Connexivum with reddish yellow lateral spots on dorsal surface, which as a rule extend to the margin and form a continuous reddish yellow edging to the abdomen. Length 19 to 23 mm.

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* In a recent paper Neiva proposes re-establishing the generic name *Triatoma*, Wolf, 1802, (in Laporti) for *Conorhinus*, Laporte, 1833, on the grounds of priorty. The authors are informed by Mr. Distant, in a private communication, that he sees no reason for thus altering a well established and universally familiar name.

According to de Geer, *Conorhinus rubrofasciatus* is a true Oriental species which has spread to other parts. Neiva, who has recently studied all the known museum specimens, gives its distribution as follows:—Brazil, chiefly in the towns along the sea coast, such as Para, Bahia, Rio de Janeiro, and Santos; Haiti; Argentina; Guyana Franceza and St. Thomas; China; India in various localities; Philippine Islands in various localities; Madagascar; Sierra Leone; Mauritius; Diego Suarez; Zanzibar; Tanga; Sumatra; New Guinea; Indo-China in various localities; Borneo; Java; Seychelles; Ceylon; Angola; Singapore; Japan and Formosa.

Geographical Distribution

Distant gives its distribution as follows:—Sylhet (Stockholm Museum) Bor Ghat (Dixon), Bombay (Leith); Calcutta and Mysore (Indian Museum); Ceylon (Green); Andaman Islands (Indian Museum); Toungoo, Mandalay (Fea). Widely distributed throughout the Malay Peninsula and Malayan Archipelago; recorded from Madagascar; West Africa (Distant Collection); and generally found in the Southern Neartic and Northern Neotropical Regions and in the Antilles.

There appears to be some doubt as to whether *Conorhinus rubrofasciatus* occurs in West Africa. Bagshawe, in the *Sleeping Sickness Bulletin*, states that Mr. Guy Marshall, Director of the Imperial Bureau of Entomology, has not so far received any specimens from the African Continent.

Neiva states that he was unable to find a single specimen in any of the museums in the United States which he visited. Champion, in the *Biologia Centrali-Americana, Rhynchota*, vol. ii., identified three specimens from Mexico as *rubrofasciatus*, but he appears to have some doubt as to the accuracy of the determination. Neiva considers the Mexican forms represent a variety which he describes under the name *mexicana* (see below).

Bionomics and relation to disease

In Madras *Conorhinus rubrofasciatus* in its adult stage is a familiar insect, as it frequently enters houses at nights; the majority which do so are males. If the alimentary tracts of specimens caught in this way are dissected out, they will be found to contain partially digested mammalian blood, and the question arises as to where this food is obtained. On one occasion the authors found a dead female in a nest of the South Indian squirrel, *Funambulus palmarum*, and the presumption is that *rubrofasciatus* feeds either on this animal or on some other small mammal. The squirrel has the habit of roosting in holes in the banyan tree in Madras, and it is possible that the bug lives in these places. Although a vigorous search has been made for the early stages in holes in the ground and about the roots of trees, etc., they have never been seen in any of the localities in which the adults are common; it therefore seems probable that it does not lay its eggs on or near the ground, and that it is arboreal in habit.

It has been suggested that *rubrofasciatus* may possibly prove to be the invertebrate host of the parasite of Kala Azar in Madras. This suggestion was based mainly on the statements of some of the inhabitants of Georgetown, Madras, where Kala Azar is prevalent. These people stated that they had seen the bug in a few instances in their houses and had been bitten by it. One of the authors made a careful investigation into this question and found that *Conorhinus rubrofasciatus* was unknown to the majority of the occupants of houses where cases of Kala Azar had occurred; neither the adult insect nor any of its early stages were found in any of the several hundred houses examined. This bug is a large insect, and were it common it could hardly escape detection. The senior author has fed a large number of adults and nymphs of *rubrofasciatus* on himself and has recorded the effect of their bites. At the moment the puncture is made a slight sting or prick is felt; if the insect is caught carelessly it may cause a severe prick. Twelve hours after the bite a large erythematous patch about the size of a shilling appears at the site of the puncture; it remains in an inflamed and extremely irritable condition for about a fortnight and then fades away; a small nodule about the size of a No. 6 shot persists for about a month. The irritation produced by the bite, if it is anything like what the senior author has experienced, could not escape observation.

Conorhinus rubrofasciatus has been bred at the King Institute for the last two years. During this time all the stages from the larva to the adult have been kept in test tubes and regularly fed on rabbits, to which host they have readily adapted themselves. This fact strongly suggests that this bug is to a large extent a blood-feeder, but as to whether it is entirely so cannot be settled with certainty until the natural habitat of the early stages has been discovered. There is no proof that it attacks man in Madras unless under very exceptional circumstances, as when it is carelessly handled.

In captivity all the stages, but more particularly the adults, exhibit a peculiar habit when about to suck blood. After erecting the proboscis the insect slowly lowers it towards the skin and then makes a sudden forward thrust with its body; this habit, which was noted by Darwin in the case of *C. infestans*, recalls the behaviour of many predaceous reduviids when they are about to pierce an insect with the proboscis.

In Madras *Conorhinus rubrofasciatus* is commonly infected with a flagellate, *Crithidia conorhini*, Donovan. In Mauritius Lafont has found eighty per cent infected with a similar flagellate. He states that he has succeeded in infecting rats and mice with a trypanosome by inoculating them intraperitoneally with the flagellates from the alimentary tract of the bug. In the case of rats the parasite was only found in the peritoneum up to thirty hours after inoculation and never in the peripheral blood; in mice the flagellate appeared in the peripheral blood six to seven hours after inoculation. The infection lasted from one to five days, after which it disappeared; most of the mice died. Lafont draws attention to the possible rôle this flagellate may play in the case of man. In Mauritius this bug is occasionally seen in houses, and has been caught in the act of biting. It is not stated, however, whether the early stages of the bug are to be found in houses as in the case of *Conorhinus megistus* (see below).

Early stages

The *egg* (Plate LX, fig. 2) of *Conorhinus rubrofasciatus* is rounded at one end and flattened at the other, which forms a kind of operculum; when first laid it is of creamy white colour, but it becomes lemon yellow some time before the larva emerges. It measures 2 mm. in length and 1 mm. in breadth. The incubation period lasts from twenty to thirty days according to the temperature. The *larva* (Plate LX, fig. 3) has a bright lemon yellow abdomen and dark brown head and thorax; the distal half of the last antennal joint is light brown. It is very active and will suck blood about three days after hatching out. The larval stage lasts from ten to fifteen days, and during this time one feed of blood is taken, very occasionally two, and then only if the first is an incomplete feed. The first nymphal stage occupies from fifteen to twenty days and at least three feeds are taken during this time. The second stage lasts from forty to forty-five days and about five feeds of blood are taken. The third is completed in about thirty-five days, during which time five feeds of blood are taken, and the fourth and last nymphal period lasts another forty days, with six or seven feeds of blood. From the above observations it will be noted that in the laboratory the larva of *Conorhinus rubrofasciatus* becomes an adult in from four and a half to five months, and that during this period it will feed at least twenty times. This period of growth was completed under the most favourable conditions of food supply; it is very probable that under natural conditions blood is not so easily obtained and that the larva takes from five to five and a half months or longer to become an adult. From a large

PLATE LX

Figure 1. Larva of *Cimex rotundatus.* × 28.
Figure 2. Egg of *Conorhinus rubrofasciatus.* × 16.
Figure 3. Larva of same. × 20.
Figure 4. Second nymph of *Cimex rotundatus.* × 18.
Figure 5. Second nymph of *Conorhinus rubrofasciatus.* × 6.
Figure 6. Third nymph of *Cimex rotundatus.* × 18.
Figure 7. Third nymph of *Conorhinus rubrofasciatus.* × 6.

PLATE. LX.

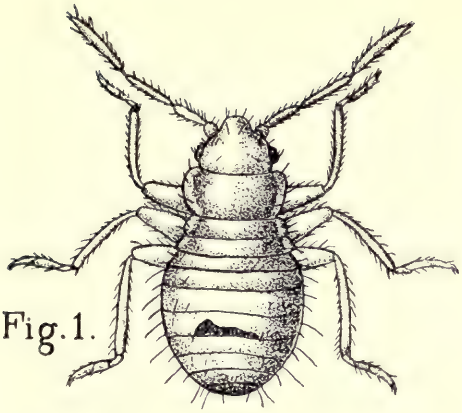

Fig. 1.

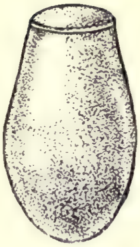

Fig. 2.

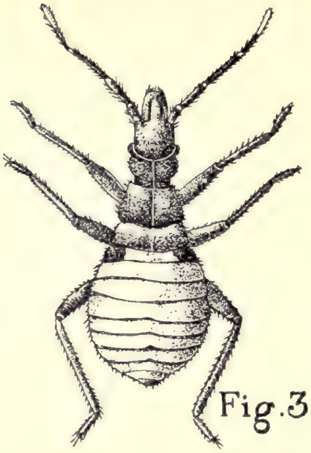

Fig. 3.

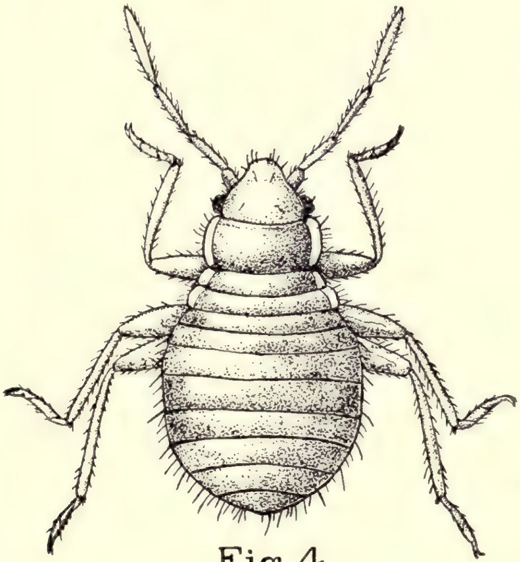

Fig. 4.

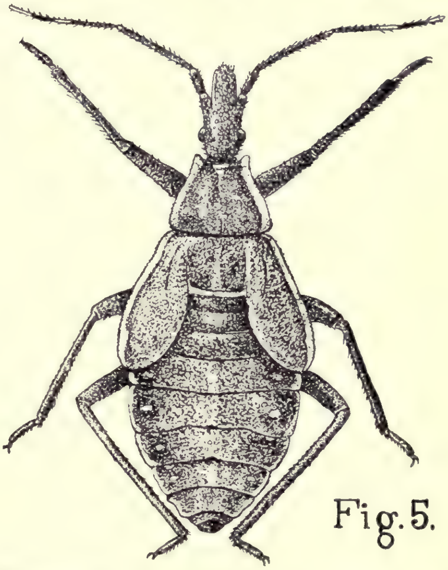

Fig. 5.

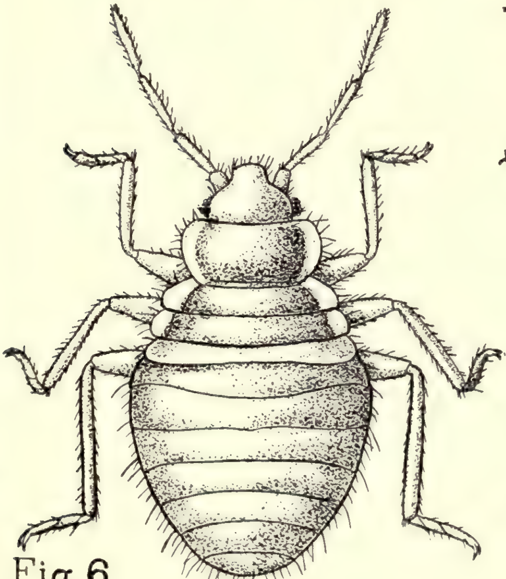

Fig. 6.

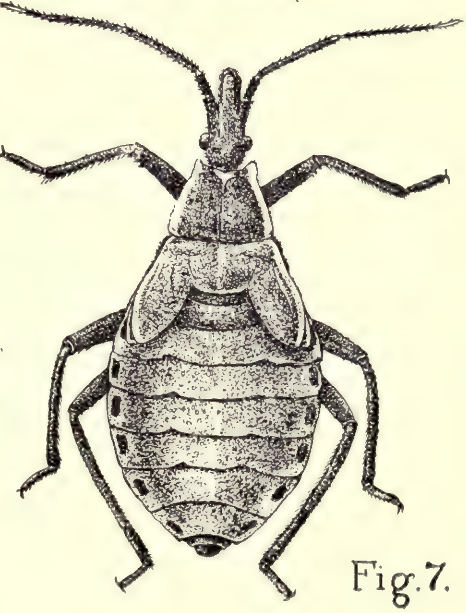

Fig. 7.

number of observations which have been carried out throughout the year with bred specimens in the laboratory, it has been found that the larvae which hatch out of eggs laid in May and June become adults in September and October; the larvae which hatch from eggs laid by these adults towards the end of October and during November become adults in February and March. The wild adults are seldom seen in houses before November, and again in June and July.

Length of life and number of eggs laid

A large number of observations have been made on the length of life and number of eggs laid by females in captivity. In each case a male was kept in the tube along with a female, and as the batches of eggs were laid they were transferred to a fresh tube. The adults were fed regularly on rabbits once a week. The longest period a female has lived under these conditions was 120 days, and during this time seventy eggs were laid in five batches of from five to thirty-one eggs; this female fed twelve times. Another female lived thirty-three days and laid 201 eggs in eight batches of from twenty-six to thirty-two eggs. The male *rubrofasciatus* rarely lives more than forty days in captivity, and during this period seldom feeds more than five or six times.

Breeding technique

It is comparatively easy to breed *Conorhinus rubrofasciatus* in captivity. It is only necessary to catch a female and to place it in a large test tube; a piece of filter paper should be placed at the bottom of the tube for the bug to rest on, and to absorb its fluid excreta, which are usually very plentiful. A day or two after the bug has been captured it should be given an opportunity to feed. This is accomplished by first drawing up the filter paper to the mouth of the tube and then either inverting it over one's arm or over the shaved back of a rabbit. If the bug is going to feed it will soon commence to suck blood, and will become replete in about ten minutes. These captured females nearly always lay fertile eggs. Once the eggs have been obtained there is no difficulty in breeding out a number of adults, mating them and obtaining their eggs without ever allowing them to leave the test tube; the tubes containing the bugs should be placed upright in small glass jars. The nymphs of the third and fourth stage are the most delicate, and if they fall into the fluid excreta are apt to die. It is, therefore, important at this stage to renew the filter paper every day or even twice a day, especially if there is a large number of bugs in each tube. From a single female captured in November, 1911, the authors have bred out large numbers of adults and the experiments are still in progress (October, 1913).

Conorhinus rubrofasciatus, variety *mexicana*, Neiva. Proboscis, head and pronotum chestnut brown; scutellum, which ends in a slender point, of the same colour. Corium and membrane dark brown; in two specimens examined by Neiva there were clear areas at the base and apex of the corium. Connexivum with dark dots separated by ochraceous lines. Ventral surface of body and legs dark brown.

This variety the type of which is in the British Museum, is found in Mexico; its habits and early stages are unknown.

Conorhinus megistus, Burm. (Plate LIX, fig. 2). Dark brown to black. Pronotum broadly expanded, with two broad raised red lines extending from the middle to the posterior border, and a red spot on the postero-lateral angles of pronotum. At the anterior border of the pronotum there are six short spines, three on each side; the most anterior are the longest and project on each side of the eyes; two are situated further back, one on each side of the middle line at the origin of the two admedian ridges; the third spine is situated on a ridge at the junction of the middle and anterior third of the pronotum just above the first pair of legs. Scutellum dark brown with two short red lines converging towards the apex, where they meet; apex red, turned upwards and bluntly rounded off. Corium and membrane fuscous, the former with one or more red streaks. Connexivum with six well marked bright red lines, broader in the male; in both sexes the lines extend round to the ventral border. In the male the last segment, except for a central black mark, is entirely red. Length 30 to 32 mm.

This large dark species is widely distributed in Brazil. In the States of Minas Gaeras, Sao Paulo and Motto Grosso it is popularly known as the 'Barbeiro' (barber), and in the southern parts of the latter state as 'Chupanca' or 'Chupao'; in Rio Grande de Sul it is spoken of as 'fincao' and in some of the northern states of Brazil as 'bicho de parede' (wall insect). Neiva states that *megistus* also occurs in British Guiana.

Relation to disease

As has already been noted *Conorhinus megistus* is the invertebrate host of *Trypanosoma cruzi*, Chagas. In certain localities in the State of Minas Gaeras the disease caused by this parasite often attacks the entire population; children develop it during the first years of their lives and then either die or pass into the chronic form, which may last a long time. The parasite has been successfully transmitted by the bite of *Conorhinus megistus* to monkeys, guinea pigs, rabbits and dogs, to all of which it is pathogenic. Chagas believes the parasite has two forms of development in its invertebrate host. In one there is a simple culture of the parasite in the alimentary tract of the bug. In the other it undergoes marked developmental changes and as a result invades all the organs, including the salivary glands. The fluid excreta of infected bugs, which often contains flagellates, have been proved to be infective when inoculated into animals.

Bionomics and early stages

The bionomics and early stages of this important bug have been fully described by Neiva, a résumé of whose observations is given here. *Conorhinus megistus* is almost entirely a domestic insect. The adults enter inhabited houses, but never those which have been abandoned. In houses which are old and badly kept they are to be found in cracks and holes in the walls, where they lay their eggs; the early stages, which are wingless, crawl out of their resting places in the walls as soon as the lights are put out and make their way to the beds of the occupants of the house. The adults behave in the same manner, but as they are powerful fliers they can reach people who sleep in hammocks. The bite is said to be painless and to leave no mark; this is quite unlike the bite of *Conorhinus rubrofasciatus*, which in the case of some people leaves a distinct mark for weeks. In captivity *megistus* feeds readily during the day time.

The *egg* of *megistus* is of a creamy white colour and is similar in shape to that of *rubrofasciatus*. They are laid in batches of from eight to twelve eggs, and as many as forty-five such batches may be laid. According to Neiva they hatch in from twenty-five to forty days. The larva is of a uniform light colour when it emerges, becoming darker later; it takes its first feed from five to eight days after emerging from the egg, and the second from the fifteenth to the twentieth day; it changes its skin (first nymphal stage) after about forty-five days. The second moult takes place during the second or third month, and the third during the fourth or sixth month. The fourth moult occurs about the 190th day after the larva has hatchd out from the egg; this stage lasts at least forty-two days. Neiva states that this time is the most critical period in its life, and that large numbers die. After the next moult the adult stage is reached, and eight days later they are ready to suck blood; egg laying commences about the fifty-fifth day after the first feed. One female kept under observation by Neiva for about three and a half months laid 218 eggs in thirty-eight batches. Under favourable conditions of food supply the cycle from egg to egg is completed in about 324 days.

Conorhinus sanguisugus, Lec. General colour dark brown with pink streaks and spots. Pronotum with two short admedian raised pink lines, and pink lateral edges. Anterior border of pronotum with a short pink spine on each side. Corium dark brown with some pink at the base; membrane light brown. Connexivum brown with light pink stripes extending for a short distance round to the ventral surface. Legs and rest of abdomen brown. From the United States, particularly the valley of the Mississippi.

The egg of *sanguisugus* is similar to that of *rubrofasciatus*. The early stages, which have been described and figured by Kimball and Marlatt, are very similar to those of the Oriental species. In America the adult insect is called 'the blood-sucking Cone nose' or sometimes the 'Texas bed bug.' It comes into houses, but its normal food appears to be the body juices of other insects; it has been seen feeding on the bed bug, *Cimex lectularius*. Kimball found it in poultry houses and horse stalls. Marlatt states that the bite of this bug often causes severe constitutional symptoms. In a recent paper Morrill states that in many parts of Arizona *sanguisugus* takes the place of *Cimex lectularius* and is common in houses.

Neiva records a variety *ambigua* from Florida, U.S.A., which is smaller and paler than the type; the stripes on the connexivum are more of an ochraceous colour.

Conorhinus uhleri, Neiva. General colour dark mahogany. Head, including proboscis and antennae, of the same colour. Pronotum dark brown, lighter on the tubercles and sides; there are two admedian raised lines on the pronotum which diverge posteriorly. Scutellum dark brown, apex light. Corium dark brown with light markings at the base. Connexivum with dark spots not reaching to the edge. Ventral surface of the body dark brown; legs light brown. In the male the spots on the connexivum are not so well marked as in the female, and its general colour is much lighter.

This species is found in Texas, Arizona; Tugson, Oracle, Hot-spring Sta. Catalinia, California; San Diego. New Mexico, Messila Park. It is said to frequent human houses and to suck blood.

Conorhinus neotomae, Neiva. Proboscis reddish brown; antennae dark brown, last segment light. Anterior lobe of pronotum a little accentuated; the posterior angles with light spots; median portion with two raised ridges diverging posteriorly. Scutellum dark brown throughout. Corium dark brown with a red spot in the middle, and another situated at the apex; membrane dark. Connexivum with black dots and light reddish brown streaks. Femora light brown with a reddish tinge; the tarsi the same.

This species is found in Arizona; Tugson. Texas; Weid-Brownsville (Los Borregos). The immature stages were found by Schwartz in the nest of the rat, *Neotoma albigula*; all were replete with blood, presumably that of the rat.

Conorhinus brasiliensis, Neiva. Head, proboscis and antennae dark brown. Pronotum dark brown with two light stripes beginning in the centre and diverging posteriorly; sides and posterior angles light. Scutellum dark, ending in a blunt point. Corium brown and dotted with black; membrane brown. Connexivum with yellow spots separated by dark stripes. Legs dark brown with three yellow rings, two on the femora and the third at the apex of the tibia.

This species resembles *Conorhinus infestans*, Klug, (Vinchucha) the Pampas bug of Darwin, of which no description is available; it can be distinguished from it by the fact that the latter has two yellow rings at the base of the femora. *C. immaculata*, Erichson, another very similar species, has uniformly coloured legs.

C. brasiliensis is commonly known as the 'bicudo' in Caicó, Rio Grande do Norte, where it is found; it is said to enter houses and to rest in cracks in the walls, coming out at night to suck blood. Its bite is said to be painful and to produce large subcutaneous swellings.

Conorhinus flavida, Neiva. Head black, spotted with yellow; proboscis and antennae yellow. Pronotum black with yellowish spots and a well marked tubercle on the posterior border. Scutellum dark with a light apex. Corium yellow with sparsely scattered yellow spots; membrane yellow. Connexivum yellow with dark spots reaching to the margin. Ventral surface of abdomen dark brown. Fore and mid femora armed with spines. Length 24 mm.; breadth 8 mm. From Cuba. Its habits and early stages are unknown.

Conorhinus heidemanni, Neiva. Head, proboscis and antennae dark brown. Pronotum lobed, brown with three well marked black stripes down the centre. Scutellum black with the apex brown. Corium brown with a large black spot, and in some specimens a yellow one in addition. Connexivum black with red stripes. Ventral surface of abdomen brown; legs dark brown, tarsi light brown. Length 18 to 22 mm.; breadth 7 to 8 mm. From Belfrage, Texas; Illinios; Pennsylvania; Tenesse.

This species is said to enter houses; one specimen was caught in the act of biting a child on the lip.

Conorhinus occulata, Neiva. Head, proboscis and antennae brown. Pronotum, anterior portion black and with tubercles, posterior portion brown. Scutellum dark with light apex. Corium with base and subapical portion light, a black spot in the centre, and another at the apex. Connexivum ochraceous with black spots. Ventral portion brown; dark legs brown; tarsi light brown. Length 18 mm.; breadth 7 mm. From Texas. Its habits are unknown.

INTERNAL ANATOMY OF CONORHINUS

The alimentary canal

The internal structures of *Conorhinus rubrofasciatus* are simple and easy to recognize. The *alimentary* canal shows the usual divisions, and, like that of the bed bug, to be described presently, is remarkable for the low insertion of the Malpighian tubes. The *pharynx* (Plate LXIV, fig. 5) is elongate, corresponding with the shape of the head, and is boat-shaped, the anterior end being much narrower than the posterior. It consists of two chitinous plates, of which the ventral is the stoutest and most strongly concave; the dorsal plate fits inside the ventral one and is in apposition with it in the position of rest, but can be pulled away from it by a series of strong dilator muscles, which pass from its dorsal surface upwards and outwards to the inner surface of the wall of the head cavity. The oesophagus emerges from the posterior end of the pharynx as an extremely delicate tube, and passes through the neck and the thorax. At its termination the thickness of the wall of the gut is greatly increased, and the wall itself thrown into a number of thick folds (Plate LXII, fig. 10), forming a *proventriculus*, a structure which is absent in the bed bug. The epithelium at this part is composed of columnar cells. The *mid-gut* commences as a saccular swelling of considerable size, equal to about one-fourth the total length of the alimentary canal. In the resting condition the lumen is occupied by a collection of small bubbles of gas, with a considerable amount of a reddish brown pigment; immediately after feeding the chamber is greatly distended with fresh blood, which is strictly limited to this swollen part of the gut. As digestion proceeds the colour darkens and the contents come to have a thick treacly consistence. Posterior to the saccular portion of the gut the lumen is very much constricted, and always contains a large amount of black debris. The tube is convoluted and situated mainly in the posterior part of the abdomen. The rectum is very sharply marked off from the rest of the gut by its creamy white colour. It is pear-shaped, with the broad end directed forwards, and is marked throughout its surface with numerous coarse striations, indicating the course of the circular bundles of muscles fibres in its wall.

The four Malpighian tubes enter the gut just anterior to the commencement of the rectum.

The salivary apparatus

The salivary apparatus resembles that of the bed bug, to be described in more detail further on, and consists of two pairs of glands with fine ducts and a salivary pump. The posterior pair of glands, corresponding to the cardiac glands of *Cimex*, are small oval bodies situated on each side of the proventriculus, to the wall of which they are attached by some delicate fibres (Plate LXII, fig. 10). The anterior pair, corresponding to the ovoid glands, are slightly larger, and lie free in the anterior end of the abdomen. The delicate ducts of these glands have not been traced through the neck; in the head they are found lying one on each side of the salivary receptacle, eventually fusing to form a short median common duct. As in the bed bug, there is some doubt as to the ultimate course of the duct of the ovoid gland, which divides into two branches shortly after its origin from the gland. The *salivary receptacle* or pump (Plate LXIV, fig. 6) is a remarkable and interesting structure. It consists of a small conical chitinous chamber, opening by an elongate channel, with a fimbriated margin, at the point at which the mandibles of the two sides come in contact with one another, and closed posteriorly by a stout piston rod, which is connected with the broad distal end of the chamber by a stout but flexible membrane. On each side of the chamber there is a stout rod of chitin, loosely attached to the ventral wall of the pharynx; these are connected with the piston rod which lies between them by a series of obliquely directed muscles, the result of the contraction of which will be to withdraw the rod from the chamber, and therefore to draw up the saliva from the glands.

Reproductive organs

The female organs of reproduction are of a simple type, and present none of the extraordinary features which are found in *Cimex*. Each ovary consists of seven ovarian tubes, each of which, in the mature female, shows four follicles; at the time the lowest follicle contains a ripe egg the one next above is also approaching maturity, so that the second batch of eggs can be laid a very short time after the first. On each side of the common oviduct there is a small white or cream coloured spermatheca, shaped very much like the haltere of a Dipterous fly, but with a much stouter stalk. The spermathecae are filled with a dense mass of large sickle-shaped spermatozoa.

Conorhinus is best dissected by the following method. Cut off the egs and wings as close to the body as possible, and then take the bug between the finger and thumb of the left hand. Take a pair of fine scissors in the right hand, and cut all round the lateral margin of the abdomen, removing the entire margin on each side, but stopping short at the anal end. Now place the specimen in a paraffin trough with its ventral surface uppermost, fasten it down by two pins through the lateral margins of the thorax, and flood it with saline solution. Take a hooked retractor needle, and insert it in the notch between the posterior end of the thorax and the anterior end of the abdomen, that is, in front of the first abdominal sternite. With a slow and steady pull the whole of the ventral wall of the abdomen can be removed from before backwards, the connecting tracheal twigs being severed as it is retracted. The flap should be pinned out behind the dissection.

Dissection

The whole of the contents of the abdomen are now exposed. The mid-gut and rectum are easily recognized by the characteristic colour of their contents; the ovaries can be freed by detaching the apical threads, and reflected backwards out of the way. To obtain the salivary glands, cut through the neck with a pair of sharp scissors, and then pull the proventriculus, with the cardiac glands attached, out of the thorax; the anterior pair of glands are attached to the proventriculus by a few fine fibrils, and can be drawn out and removed in a wide pipette.

FAMILY CIMICIDAE

Head short and broad; the proboscis lies in a groove on the ventral surface of the head and thorax; ocelli are absent; *elytra short and broad, leaving most of the abdomen uncovered. Tarsi three-jointed.* (Distant).

According to Distant the family Cimicidae contains the four genera *Cimex*, *Oeciacus*, *Cacodmus* and *Haematosiphon*; to these must be added the genus *Loxaspis* recently created by Rothschild for a species parasitic on a bat. The genus *Cimex* is the only one which contains important blood-sucking species.

GENUS CIMEX,* L.

Head short and broad; antennae four-jointed, the apical joints slender. Prothorax semilunar in shape with its anterior angles considerably

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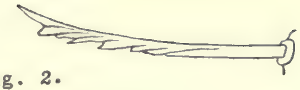
* There has been considerable dispute regarding the generic name of *lectularius*, L.; the literature dealing with the subject is given in Girault's *Bibliography of the Bed Bug, Cimex lectularius*, to which the worker is referred for further details. Dr. C. Wardell Stiles has made a careful study of the synonomy of this insect and has decided that *lectularius* is the type of *Cimex*, Linnaeus. The authors see no adequate reason for altering the generic name now familiar to every one; the generic names *Acanthia Klinophilos* and *Clinocoris* are therefore rejected.

PLATE.LXI.



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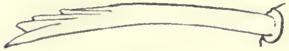
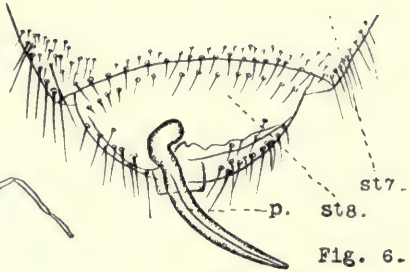


Fig. 4.



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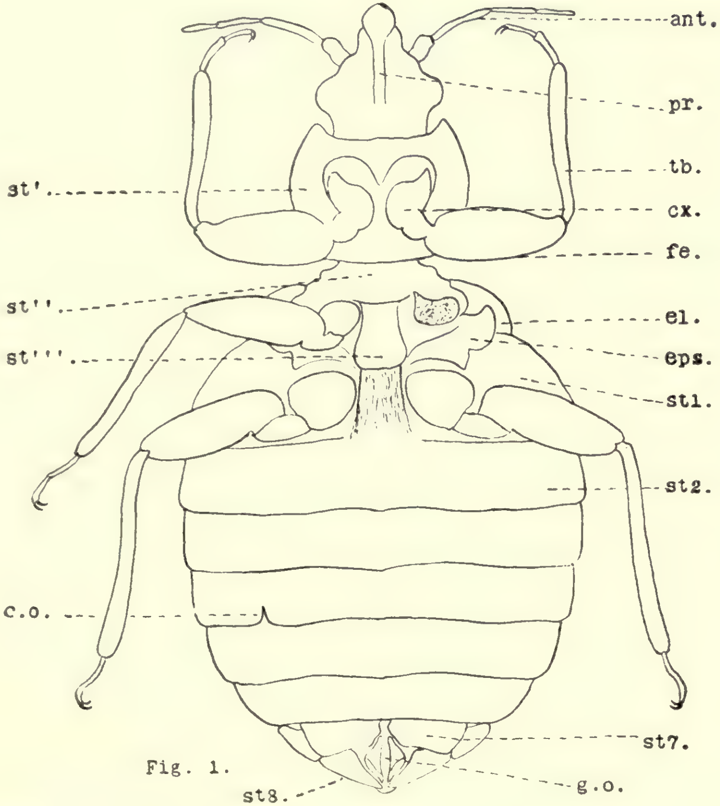
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Fig. 1.

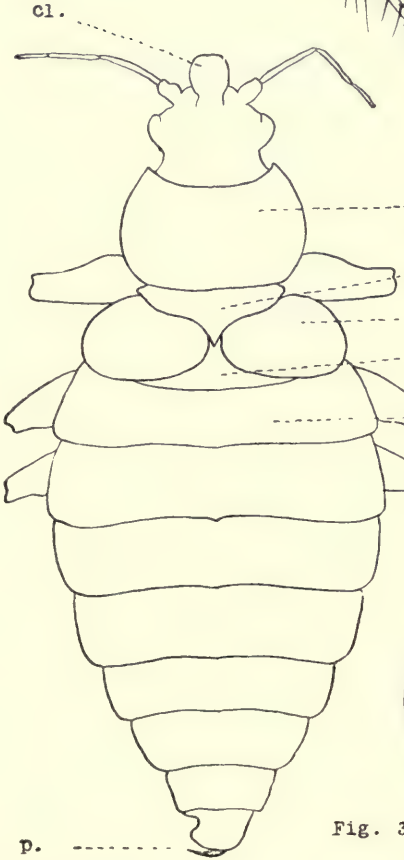
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Fig. 3.

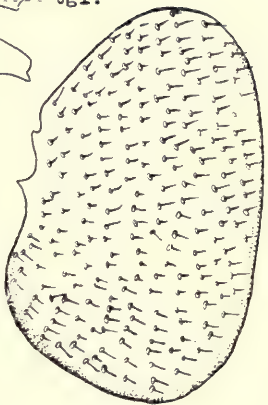


Fig. 5.

PLATE LXI

Figure 1. *Cimex rotundatus*, ♀, ventral aspect. st′., prosternum. st″., mesosternum. st‴., metasternum. c.o., the copulatory orifice, leading to the organ of Berlese. ant., antenna. pr., proboscis. tb. tibia. cx., coxa. fe., femur. el., elytra. eps., episternum. st. 1., first abdominal sternite. st. 2., second abdominal sternite. st. 7. and st. 8., the seventh and eighth sternites. g.o., the genital orifice.

Figures 2 and 4. Examples of the serrated hairs of *Cimex*.

Figure 3. *Cimex rotundatus*, ♂, dorsal view. cl., clypeus. pn., pronotum. msn., mesonotum. mtn., metanotum. tg. 1., the first abdominal tergite. p., the penis.

Figure 5. An elytron of *Cimex*.

Figure 6. The terminal portion of the abdomen of *Cimex rotundatus*, ♂, ventral view. st. 7. and st. 8., the seventh and eighth sternites. p., the penis.

extended; the elytra are rudimentary and lie over the metathorax. The abdomen is uncovered and consists of eight segments. Legs slender; anterior tibiae more than twice as long, and the posterior three times as long, as the tarsi, which are three-jointed.

The interest attaching to this genus centres round the bed bugs, of which there are three known species, *lectularius*, L., *rotundatus*, Sign., and *boueti*, Brumpt; the latter is a doubtful species and may prove to be *C. pipistrelli*. *Cimex hirundinis*, *C. columbarius* and *C. pipistrelli* are as their names imply, parasitic on the swallow, pigeon and bat respectively.

EXTERNAL ANATOMY OF CIMEX

The external anatomy of *Cimex* differs in so many respects from that of the other Rhynchota that it merits a separate description. The following account refers especially to the Indian species, *rotundatus*, there being few divergences, except in the prothorax, between this species and *lectularius*. As regards the mouth parts, the account will apply generally also to *Conorhinus*, the disposition of the parts being closely similar in the two genera, as will be evident from the figures.

The body of the bed bug is strongly flattened in the dorso-ventral direction, and is divided into head, thorax, and abdomen, the two latter regions showing distinct segmentation. The abdomen is the largest of the three regions, and is broad and oval in the female, oval and pointed posteriorly in the male (Plate LXI, figs. 1 and 3).

The head

The head has the shape of a flattened and bluntly pointed pyramid, and is attached to the thorax without the intervention of a neck. The eyes are situated on the posterior third of the lateral borders, and appear as small dome-shaped elevations, conspicuous on account of their black pigmentation. The antennae are inserted in front of the eyes, also on the lateral borders. Each antenna consists of four elongate and cylindrical joints, of which the basal one is much stouter than the rest; the second joint is the longest, the fourth or terminal joint only a little longer than the basal one and thinner than the others. In the resting position the antennae are directed outwards and a little forward.

The proboscis

The *proboscis* commences at the distal end of the head, and arches at once downwards and backwards from its origin to lie on the ventral surface, reaching as far backwards as the origin of the first pair of legs. Dorsal to its point of origin there is a small two-jointed flap, the *labrum* (Plate LXII, fig. 9), which is arched from before backwards and also from side to side, so as to form a covering for the constituent parts of the biting apparatus as they emerge from the head. The basal and largest of the two joints is heart-shaped, and is directly continuous with the chitin of the head wall; it may represent the clypeus. This flap can be raised and lowered with the rest of the proboscis. Both joints are covered on their external surface with small serrated hairs.

The proboscis is a long cylindrical and pointed organ, which, though it points backwards in the resting position, can be erected until it points downwards and forwards. It consists of a pair of mandibles, a pair of first maxillae, and a labium, which, as in the simpler Diptera, serves as a sheath for the piercing parts. There is no epipharynx or hypopharynx, the food channel being formed by the two mandibles, which also serve to convey the saliva to the wound.

The labium

The *labium* (Plate LXII, fig. 7) is the only part of the proboscis which can be seen without dissection, as the other appendages are concealed in an almost closed groove on its anterior surface. It consists of four joints, the first of which is the broadest and shortest, has a semi-membraneous wall, and lies in a V-shaped notch on the ventral side of the proboscis aperture; the second and third joints are each about twice the length of the first and rather narrower, have well chitinized walls, and are separated from one another and from the basal joint by loose membraneous areas. The distal joint is narrow and terminates in a blunt point. The method of articulation of the joints with one another permits of the shortening of the whole organ which takes place when the piercing stylets enter the skin.

The labium is a hollow organ with a chitinous wall, the internal space being continuous with the haematocoele of the body. It contains a pair of longitudinal muscles, passing between the several joints and serving to effect the necessary retraction, a pair of tracheae, and many hypodermal cells, which are larger than one usually meets with in such situations, arranged around the wall. The dorsal surface of the organ—inferior when in the position of rest—is invaginated throughout its whole length to form a groove for the reception of the mandibles and maxillae. The two lips of the groove meet, or even overlap, in front. The walls of the groove are composed of chitin as thick as that of the rest of the labium, and there is no membraneous interval separating the labial gutter from the posterior part of the wall.

The *mandibles* have entirely lost what may be supposed to have been their original function, and have become modified to form two channels,

PLATE . LXII.

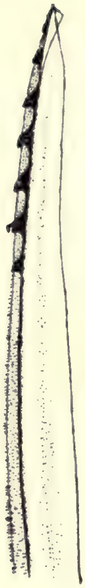


Fig. 1.

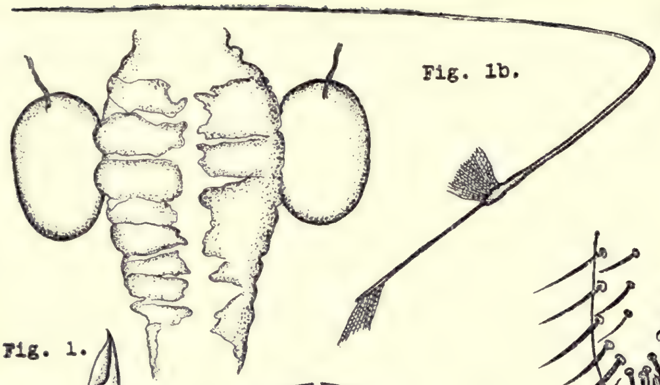
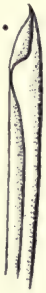


Fig. 10

Fig. 1b.



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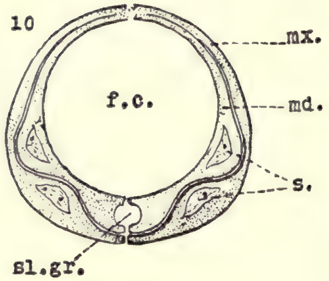
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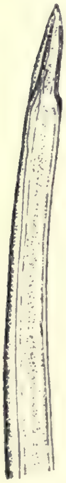
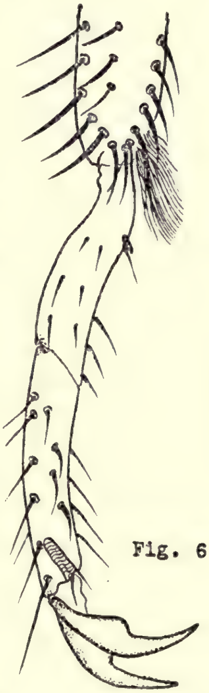


Fig.1a.



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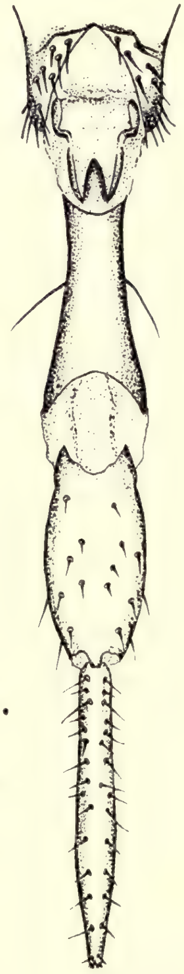

Fig. 7.

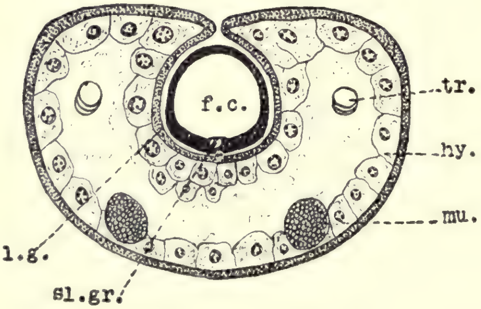
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Fig. 5.

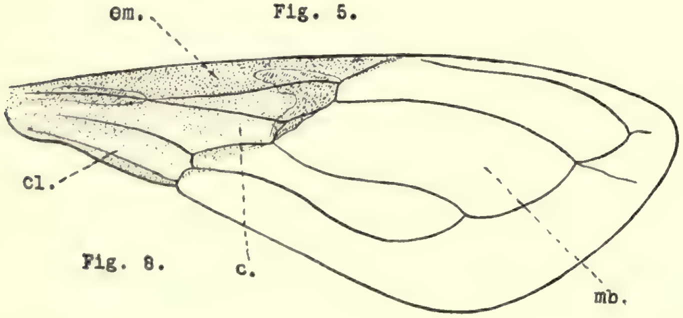

Fig. 8.

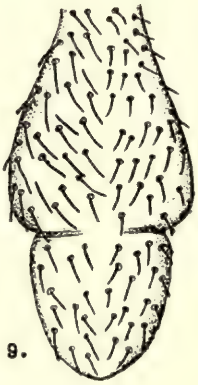

Fig. 9.

PLATE LXII

Figure 1. The distal end of the maxilla of *Conorhinus rubrofasciatus*, showing the cutting teeth. × 490.

Figure 1a. The distal end of the mandible of the same. × 490.

Figure 1b. The maxilla of *Conorhinus*, showing the positions of the muscle attachments.

Figure 2. The distal end of the mandible of *Cimex rotundatus*. Note the absence of teeth, and the flange; on the other mandible there is a corresponding excavation, the two fitting together. × 450.

Figure 4. A cross-section through the proboscis of *Cimex rotundatus*, to show the constitution of the food channel. The mandibles lie internal to the maxillae, and form a closed tube, the distinction between the two lateral halves of which cannot be clearly defined. The maxillae lie outside, fitting closely to the mandibles. s., cellular spaces in the mandibles and maxillae; note how the convexity of one organ fits into the concavity of the other. f.c., food channel. sl.gr., salivary groove in the mandibles. The labium is not shown. Very highly magnified.

Figure 5. A cross-section through the whole of the proboscis of *Conorhinus rubrofasciatus*. l.g., the labial gutter in which the mandibles and maxillae lie. f.c., the food channel (separate parts not shown). sl.gr., salivary groove. tr., trachea. hy., hypodermal cells, of conspicuously large size in this situation. mu., retractor muscles, by means of which the labium is withdrawn when the piercing parts enter the skin. × 500.

Figure 6. The terminal portion of the leg of *Cimex rotundatus*. Note the pair of claws, and the peculiar fringe of hairs at the base of the tibia.

Figure 7. The labium of *Cimex rotundatus*, seen from behind. The first of the four joints is semi-membraneous, and is not easily seen in cleared preparations. × 132.

Figure 8. The wing of *Conorhinus rubrofasciatus*. em., embolium. cl., clavus. c., corium. mb., membraneous area. × 7.

Figure 9. The labrum of *Cimex rotundatus*, showing the two joints, which are bent so as to cover the basal part of the proboscis.

Figure 10. The proventriculus and cardiac salivary glands of *Conorhinus rubrofasciatus*; the villi into which the wall is thrown are indicated by the dark shading, as seen in a stained preparation.

one of which conveys the food from the wound to the pharynx, while the other conveys the saliva in the reverse direction. The condition is comparable to that found in the fleas (page 438).

The mandibles

Each mandible is a long thin slip of yellow chitin, bent upon itself about its middle, the position of the bend corresponding to the point of emergence of the proboscis from the head. The proximal portion, therefore, lies within the head, the distal portion in the groove on the dorsal surface of the labium. The proximal portions lie on each side of the pharynx, diverging from one another posteriorly, and have two pairs of muscles attached to their swollen basal parts; one of these pulls in an anterior direction, and may be termed the protractor, while the other pulls in a posterior direction, and may be termed the retractor. The two mandibles come in contact with one another at the anterior end of the pharynx and immediately in front of the salivary reservoir, and from this point forwards the blades are flattened and strongly concave on their internal aspects, the two together forming the walls of a canal with a circular lumen (Plate LXII, fig. 4). The posterior wall of this canal is much thicker than the rest, and at the point in the middle line where the two mandibles are in contact with one another there is a semi-circular notch on each, the two notches together forming a circular channel through which the saliva passes downwards (Plate LXII, fig. 4). External to the groove the mandible is reduced in thickness, to expand again in the lateral area, where there is a small space, running the whole length of the organ, in which is contained some cellular tissue for the nourishment of the chitin of the blade. Anteriorly the blades are very thin, and it is not possible to determine, in sections, the line of demarcation between them. In dissections the two mandibles frequently remain adherent to one another by their anterior borders.

At the distal end (Plate LXII, fig. 2) the mandibles are broadened out into flanges which interlock with one another, the opening between the two blades being the prestomum.

The maxillae

The *maxillae* are the cutting weapons with which the bug makes the wound in the skin. They resemble the mandibles very closely in shape and disposition, lying dorsal and external to them in the head, and external and closely apposed to them in the proboscis. The swollen basal part has attached to it a chitinous rod which extends backwards to the posterior part of the head, and which probably corresponds to the stipes; strong retractor and protractor muscles are inserted into it and into the basal part of the maxilla proper. At the point where the mandibles converge to meet one another and to form the food canal, the maxillae come to lie external to them, their blades becoming flattened and concave on the inner surfaces, so as to fit closely to the shape of the mandibles. On each blade there is a thickened area, within which there is a little cellular tissue, as in the mandible; this corresponds in position to the thin area of the mandible immediately external to the salivary groove.

At the distal end the maxilla is pointed, and is armed with a row of fine recurved teeth, like those on the maxillae of the Orthorraphic Diptera; as pointed out by Landois, one maxilla is a little shorter than the other.*

It will be seen from the above that the lumen of the food channel is bounded entirely by the mandibles; the maxillae lie throughout external to them, and merely assist in supporting the channel by virtue of their close approximation. The channel is not formed by the four stylets in equal part, as stated by Landois.

Mechanism of the Proboscis

The method of action of the proboscis can be observed under the binocular microscope, or even under a hand lens, as captive bugs feed readily after a few days' starvation, and do not usually attempt to leave the piece of cloth or filter paper on which they rest; the proboscis is brought into the perpendicular position, or even points forward and downward, and is applied without hesitation to the skin. The bug then remains stationary for a few seconds, during which period one can, under favourable conditions, observe that the points of the piercing stylets are actually entering the skin. Next it gives a few short forward thrusts, as a result of which the parts are driven further in, and as this occurs the labium is shortened by the approximation of its chitinous portions and the puckering of the membraneous folds between them; the second and third joints are bent backwards, thus exposing the sucking tube, within which one can see the red tint of the blood as it flows upwards to the pharynx. The distal end of the labium remains pressed against the skin. The angle between the proximal and distal portions of the mandibles and maxillae is increased to a right angle or thereabouts, and its position is advanced, that is, the appendages as a whole are thrust out of the head.

The method by which the mouth parts are brought into use is not very clear. Evidently, as Landois pointed out, the action of the retractor muscles will result in an increase in the angle of flexion, by pressing them against the head capsule, while the protractor muscles will, by thrusting the angle forwards till it is clear of the head capsule, allow the natural elasticity of the parts to assert itself, as they slip back to the position of rest. If, on the other hand, the points of the piercing stylets are fixed in the skin, alternate protraction and retraction of the maxillae will bore a hole. Once the external resistant layer has been pierced, *vis a tergo* can come into play, and the whole organ is thrust in by the muscles of the body till the layer of blood is reached. A forward thrust can be readily imparted to the proboscis in the case of the bug, as there is no membraneous neck.

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* This is not the case in *Conorhinus rubrofasciatus*.

The Thorax (Plate LXI)

The *thorax* of *Cimex* is divided into three segments, of which the first is much the largest and is the best differentiated. There are no wings, but the mesothoracic pair are represented by small elytra. The legs are well developed, but are not specially adapted to enable the bug to cling to its host as in the case of lice, or for jumping as in the fleas.

The *prothorax* is the most conspicuous segment of the body when seen from the dorsal surface. It is about twice as broad as long, and articulates closely with the head in front and the mesothorax behind. The anterior borders are concave, and embrace the posterior end of the head; the lateral borders are strongly convex, and are produced forwards into prominent angles; the posterior border is straight on both surfaces. All the sclerites are welded into a compact whole, the lateral borders, where the tergite and sternite meet, being sharp. The dorsal surface is arched, and bears many hairs, while the ventral surface is flatter, and is interrupted on each side of the middle line by an oval space for the articulation of the first leg. The two spaces are separated from one another by a prominent spur which projects between them from the front.

The *mesothorax* and *metathorax* are small and rather irregularly arranged. On the dorsal surface there is a small triangular plate, articulated in front to the prothorax, which represents the mesonotum; its posterior angle projects between the elytra. Posterior to it there is a broad plate, resembling an abdominal tergite, and lying under cover of the elytra at the sides, which forms the metanotum; it is only thinly chitinized. On the ventral surface in the middle line there is first a smooth transverse plate, corresponding to the mesosternum, and behind it, and between the coxae of the middle pair of legs, a more elongate plate, at the posterior border of which the opening of the stink glands is situated; this latter plate is regarded by Landois as a process of the mesothorax, but it appears to correspond more nearly to a metasternum. At the sides of the mesosternum there are two slight elevations, the posterior and larger of which is in front of the coxa of the second leg. External to the coxa of this leg, and lying usually under cover of the femur, there is a strong hooked process, probably representing the episternum of the mesothorax. The narrowest part of the thorax is at the junction of the first and second segments; the metathorax broadens out from before backwards and merges with the abdomen.

The wings are represented by a pair of small *elytra* (Plate LXI, fig. 5) which cover the greater part of the metanotum. Their dorsal surfaces are strongly concave, and are covered with feathered hairs. They are articulated with the lateral portions of the mesonotum.

The *legs* are of moderate strength, and show the usual joints. The coxa, trochanter, femur, and tibia resemble those of the Diptera, and are easily recognized. On the inner side of the distal end of the tibia there is a small 'aigrette' of fine hairs, arranged like a comb (Plate LXII, fig. 6). The tarsus is said to consist of four joints; the first is small, and is separated from the larger second by an oblique articulation; the third is the largest, and is separated from the second by a definite notch on the outer side of the limb, while the fourth is very small, and bears the claws. The lines of demarcation between these joints are very faintly marked. The claws are bilaterally symmetrical and simple, and are not very strong. There are no pads on the feet like those with which the Diptera are usually provided, and the bug is consequently unable to move easily on smooth surfaces.

The Abdomen (Plate LXI)

The *abdomen* consists of eight segments in each sex, with some additional sclerites modified for sexual purposes. In the male the first seven segments are simple, each consisting of a tergite and sternite, the former of which overlaps the latter at the sides; the segments decrease in width in a regular manner from the third, the abdomen being distinctly more pointed in the male than in the female.

The eighth segment is asymmetrical, having a distinct notch on the left side, for the accommodation of the penis. The latter organ (Plate LXI, fig. 6) is shaped like a large claw, broad at the base and terminating in a curved point, and is directed to the left side in the transverse plane of the body, both in the position of rest and when extended. It emerges from the abdomen through a short collar-like ring of chitin which may represent a suppressed abdominal segment.

The abdomen of the female is much rounder than that of the male, the fifth segment being about as broad as the first. The genital opening is situated on the ventral side anterior to the anus, and is bounded by the modified sclerites of the seventh segment; the sternite of the seventh segment is reduced to two small lateral plates, between which there are two larger plates, also parts of the same segment. Below these four plates, which lie in the same transverse plane, there is a pair of triangular plates, which represent the eighth sternite, and in the interval between these in the middle line another pair of much smaller plates, also triangular in shape, but with their longest sides pointing in the antero-posterior direction. The genital orifice lies between their borders. The anus opens between a small pair of plates (tenth sternite) posterior to these, so that if one counts each pair of plates as representing a segment the abdomen consists of ten in all, of which four are modified.

The copulatory orifice

The fourth sternite has upon it, about midway between the right lateral border and the middle line, a small longitudinal incision (Plate LXI, fig. 1) which marks the position of the opening into the copulatory pouch, or the organ of Berlese. If the fourth and fifth sternites are separated by traction, a small and thin oval plate of chitin is revealed lying underneath the fourth sternite; in the middle of this, and immediately opposite the upper end of the incision, there is a minute orifice, with a much puckered margin, directed in the antero-posterior plane. It is into this orifice that the organ of the male is inserted in copulation. The genital orifice at the posterior end of the body serves *only* for the passage of the ova to the exterior.

The whole of the dorsal surface of the abdomen, and most of the ventral surface also, is covered with serrated hairs, similar to those shown in Plate LXI, figs. 2 and 4. The first and second sternites in both sexes are membraneous in the median area, thus allowing for expansion of the abdominal cavity after feeding. Each unmodified abdominal segment bears a pair of spiracles, which appear as small clear areas on the ventral plates, a little distance from the lateral borders.

SPECIES OF CIMEX

Cimex lectularius, L. (Plate LXIII, figs. 1 and 2). Body flattened, reddish brown in colour and covered with fine hairs. Head short and broad; eyes well developed and of a reddish colour. Prothorax semilunar in shape with two rounded horns which extend close up to the eyes; middle portion of dorsal surface raised, with the sides markedly flattened from a point just external to the level of the eyes. Abdomen rounded and broadest at the level of the third segment.

This species is distributed throughout Europe and North America; it is also found in Suez, Egypt, the Soudan, the North West Frontier of India, China, South Africa, Australia and in some parts of West Africa.

Cimex rotundatus, Signoret (*macrocephalus*, Fieb.). (Plate LXIII, figs. 4, 6 and 7). Body flattened, dark mahogany in colour and covered with fine hairs. The head is not as broad or as long as that of *lectularius*. Prothorax narrower and shorter, and rounded to the margin. The abdomen is less orbicular and is broadest at the level of the second segment.

This bug is a tropical and subtropical species. It is distributed throughout India, Burma, Assam, the Malay Peninsula, Aden, the Islands of Mauritius, Reunion, St. Vincent and Porto Rico. It is widely distributed in Africa and is probably the common species associated there with man; the Entomological Research Committee have received specimens from the following localities:—Nyasaland: North Rukuru River, Zomba, Blantyre; N.-E. Rhodesia, various localities; Northern Nigeria: Zunguru; Southern Nigeria: Benin City. The senior author has received specimens from Sierra Leone.

At one time it was believed that the Indian species was *Cimex macrocephalus*, Fieber, and that *rotundatus* was localized to the Island of Reunion. After examining a large number of bugs from all parts of India, as well as a collection from the Islands of Reunion and Mauritius, the senior author found that the Indian bed bug was *rotundatus*; this species was described by Signoret in the year 1852, whereas Fieber described *macrocephalus* in 1857.

Bionomics of lectularius and rotundatus

Cimex lectularius and *C. rotundatus* are essentially domestic insects, and among civilized people their presence in a house is considered to be a sign of neglect of cleanliness on the part of the occupants. In tropical countries this is not always the case, for often in spite of every precaution *rotundatus* will find its way into houses, chiefly on the persons of native servants. In European countries *lectularius* is only to be found in the poorer localities in the large cities, rarely in country cottages and practically never in the houses of well-to-do people.

As its popular name implies, the bed bug chiefly lives in the bed of its host, man, all the stages collecting together in crevices and holes in the framework or among the bedding. *Cimex rotundatus*, though common in similar places also collects in large numbers in corners, cracks and small holes in walls, doors, chairs, tables, screens, etc., in fact

PLATE LXIII

Figure 1. *Cimex lectularius*, ♂. × 12.
Figure 2. *Cimex lectularius*, ♀. × 12
Figure 3. Egg of *Cimex rotundatus*. × 28.
Figure 4. Ventral surface of *Cimex rotundatus*, ♀, showing the position of opening of Berlese's organ.
Figure 5. Egg of *Cimex lectularius*. × 28.
Figure 6. *Cimex rotundatus*, ♂. × 12.
Figure 7. *Cimex rotundatus*, ♀. ×12.

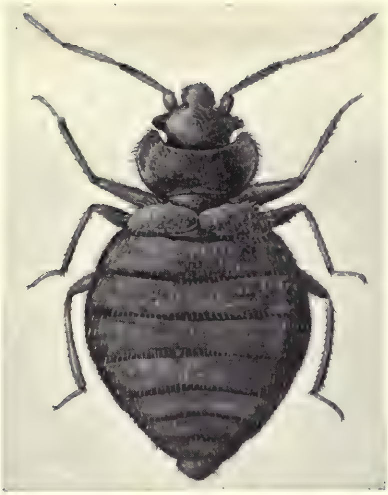


Fig. 1.

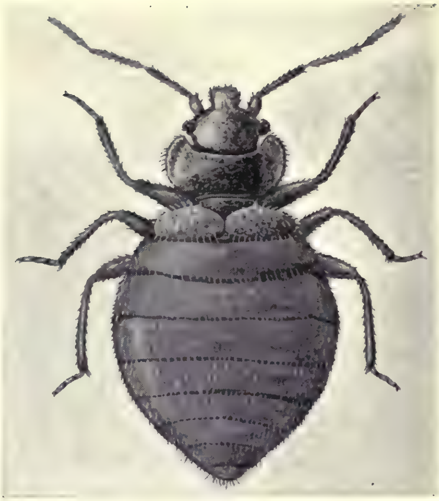


Fig. 2.

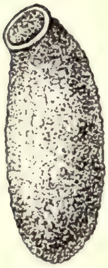


Fig. 3.

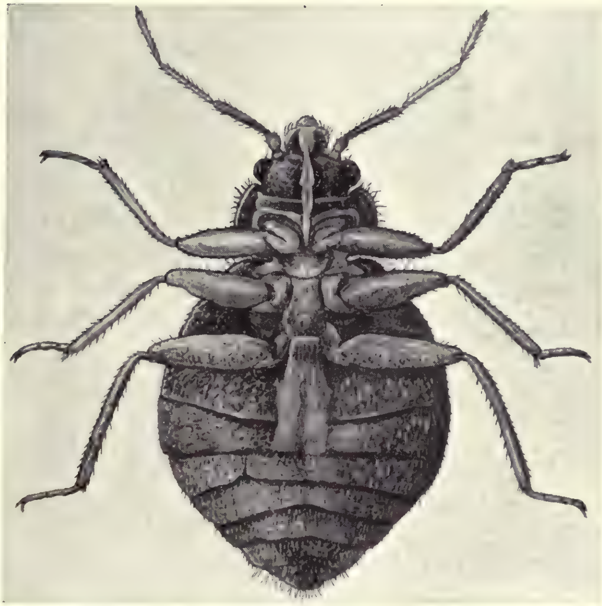


Fig. 4.

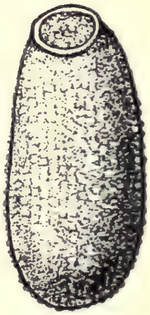
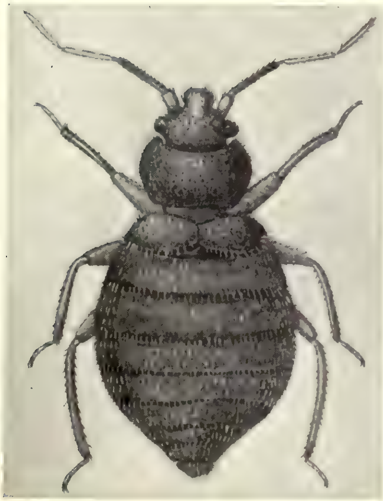


Fig. 5.



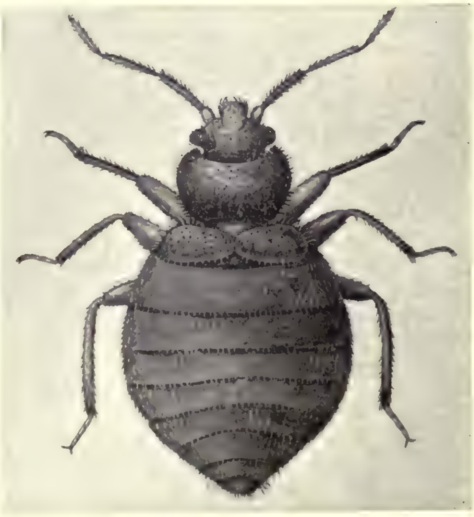


Fig. 6

Fig. 7

in any kind of furniture. As most Indians sleep on the floor the bugs crawl down from the walls and make their way to the nearest sleeper.

Although the natives periodically shake out the bugs from their beds, mats, chairs, etc., they neglect to destroy the eggs, and in a short time the pest becomes as plentiful as before. As often as not the bugs are deposited just outside the house, with the result that they make their way back either to the same room or an adjacent one, or pass into the house of a neighbour. Bug traps are commonly used in many parts of India. The simplest kind is made of a piece of wood about six inches long, four inches wide and two inches thick; about a dozen holes are bored into it, into which the bugs can crawl. The trap is placed in the bed among the clothes, and in a week or ten days it is taken out and vigorously tapped on the ground; the bugs fall out and are as a rule allowed to escape, and they often make their way back again to the house.

It is well known that *lectularius* can travel long distances. There is a record of it leaving an uninhabited house by crawling out of a window and passing along a drain pipe to an adjacent house, which it entered through a window. The senior author has noted several instances in which *rotundatus* travelled more than fifty yards to obtain a feed of blood, returning each time to its original resting place.

It is almost universally believed that the bed bug only bites the covered parts of the body and this belief is brought forward as an argument against the possibility of this insect acting as a carrier of the parasite of Oriental Sore, a disease of the skin which is usually found on the exposed parts of the body. This, however, is not the case, for the bed bug is not an ectoparasite in the sense that it clings to its host like the body or head louse; it very rarely lays its eggs in clothes, always preferring to deposit them on some fixed object. It does, however, often crawl into one's clothes, hiding itself among the folds, especially about the waist. *C. rotundatus* is a familiar object in the chairs and tables in Indian offices, the clerks bringing them from their houses. The European pith topee often becomes infested, and the Indian cloth head-dress is also a common resting place for the bug; it crawls into it when it is hung up on a nail on a wall.

Bugs which are resting in the frame work of a bed or in the bedding only bite the uncovered parts of the body; they crawl out of their resting places and make their way either to the pillow and bite the face and neck, or attack the exposed parts of the legs and arms. The senior author has seen *rotundatus* during the day time biting patients in an Indian hospital about the face, legs and arms. The swelling and irritation caused by the bites of *lectularius* on the face are now not so familiar as they were many years ago when the bug was common in houses in Europe. In Indian houses, where the occupants sleep on the floor with only a loin cloth the bug bites those parts of the body which are ordinarily covered.

In captivity both *lectularius* and *rotundatus* will feed on almost any animal; the authors have fed them on rats, cats, dogs, monkeys, rabbits, guinea pigs and calves. Both sexes are blood-suckers, though the male does not feed as often as the female. It is well known that the bed bug will live for a long time without any food; in Madras *rotundatus* has been kept alive in a test tube for four months. This fact, together with many observations made on the occurrence of *lectularius* in uninhabited houses where it was not possible for it to obtain blood, has led to the erroneous belief that the bed bug is able to subsist on the juice of moistened wood, and even on dust; such statements have even appeared in modern books on parasitology. Reference to the structure of the mouth parts and biting apparatus of the bed bug will show that it is impossible for it to ingest solid particles or to obtain moisture from wood. No food other than blood has been found in the alimentary tract of the large numbers of *rotundatus* and *lectularius* which the authors have dissected.

It has several times been stated that bed bugs will feed on each other in the absence of blood; during the course of hundreds of experiments this has never been observed in Madras, either in the case of *rotundatus* or *lectularius*. Bugs replete with blood have been placed in the same test tube with large numbers of starving adults and nymphs, but they have never been attacked, nor have starving bugs been observed to insert their proboscides into the excreta of full-fed ones.

Two very curious habits, apparently purposeless but very striking on account of the regularity with which they may be observed, are to be noted with regard to the feeding of the bed bug. Like most other blood-sucking insects it defaecates immediately after a feed, but unlike the majority, it does not pass out red blood, but only the remains of the last meal, a semi-solid sticky material; this black fluid is passed out just after the proboscis is withdrawn, and the bug has a very characteristic habit of turning round and moving backwards, in such a way that the excreta falls in the neighbourhood of the wound made by the proboscis. The second peculiarity lies in the persistence with which individuals, particularly the young stages, will return to feed after they are apparently gorged to repletion.

Early stages and life history

The bed bug undergoes an incomplete metamorphosis, the immature stages closely resembling the adults. The *egg* (Plate LXIII, fig. 3) of *rotundatus* is of a dirty white colour and ovoid in shape; the upper end has an operculum, surrounded by a narrow rim which projects more at one side than the other. The egg of *lectularius* (fig. 5) is very similar to that of *rotundatus*, but perhaps a little larger. The female bug attaches the egg by a gelatinous substance to a fixed object, usually in a crack or crevice. The *larva* (Plate LX, fig. 1) hatches out in from four to eight days or more according to the temperature.

The larva of *rotundatus* measures 1·5 mm. in length when unfed and 1·7 mm. when replete. This stage lasts from four to five days and as a rule two feeds of blood are taken in the cold weather in Madras, but the larva may feed only once. The first nymphal stage lasts from seven to eight days, during which time the bug feeds three or four times. The second nymphal stage is completed in from seven to nine days, and the third lasts another week; during each of these stages the bug feeds three or four times. The last nymphal stage lasts from ten to fourteen days with at least four feeds. In the hot weather in Madras the period from the larva to the adult takes about six or seven weeks; in the cold weather from nine to eleven weeks. Egg laying begins from ten days to a fortnight after the adult stage is reached, and during this time three or four feeds of blood are taken.

The bug usually takes about four minutes to become replete, and in the hot weather the meal is digested in from twenty-four to thirty-six hours; in the cold weather digestion is delayed, and lasts from forty-eight to seventy-two hours. If a bug is starved for ten days its mid-gut becomes filled with bubbles of gas.

Girault notes that a female *lectularius* in captivity will lay as many as 111 eggs during a period of eighty-one days; the eggs are laid in batches as in the case of *Conorhinus rubrofasciatus*, there being as many as twenty eggs in a batch. A female *rotundatus* has been kept alive for 130 days, during which time 180 eggs were laid in batches of from two to nine eggs. It is very doubtful whether a single female survives under natural conditions as long as a year; six to eight months would probably represent the limit.

Breeding technique

The method of keeping and feeding the bed bug in the laboratory has been described by the senior author. The bugs are placed in small test tubes (3 × 1 in.), and a piece of white filter paper is either crumpled or rolled up and placed at the bottom of the tube; the bugs, never more than fifteen or twenty in number, are then dropped on to the paper and the tubes are placed upright in a small jar, which is kept in a tray of water. It is generally believed that the bed bug is unable to crawl up a smooth surface such as the side of a glass; this, however, is not true, and if the tubes are not plugged with cotton wool some of the bugs will be found at the bottom of the jar, having crawled out of the tube; dead ones may even be found in the water. If regularly fed they do not often attempt to leave the tubes.

The filter paper should be regularly changed, as it soon becomes saturated with the fluid excreta and then develops moulds, and if this is allowed to happen the bugs will become infected. To accomplish this the paper with the bugs on it is drawn out of the tube with a pair of forceps, care being taken not to crush any eggs which may have been laid on it; the paper is placed in the centre of a large white enamel tray; if not disturbed the bugs do not make any attempt to leave the paper. The tube is now carefully cleaned, first washing it out with water and then wiping it with some 1 in 20 carbolic acid; it should be thoroughly dried until there is no smell of the carbolic left. To replace them each bug is grasped with a fine pair of forceps lightly across its abdomen, and dropped on to the fresh paper at the bottom of the tube by tapping the forceps against the edge of the glass. In this way all the bugs can be changed in a very short time, and there is little or no danger of any of them escaping. If there are any eggs on the old piece of paper it should be placed at the bottom of a glass jar which is standing in water. As soon as the larvae hatch out they are transferred to another tube containing some fresh filter paper. This is accomplished with the aid of a fine brush, never with forceps; the larvae are easily brushed up and then placed on the paper in the tube. After many years of experience this has been found to be the most satisfactory way of breeding and keeping bugs, and if the paper is regularly changed and all dead bugs removed, the majority will live for long periods.

Method of feeding bugs

Both the adults and immature stages can be readily fed if kept in the above way. It is only necessary to draw the filter paper on which they are resting to the mouth of the tube, and then to invert it over any part of the skin of the selected host. In a very short time they will crawl down to the skin and begin to suck blood. The adults and nymphs never leave the paper, but remain resting on the edge while they feed; the larvae, on the other hand, very frequently leave the paper and crawl about on the skin before settling down to suck. As a rule they return to the paper when replete with blood, but sometimes they have to be brushed up and placed on the paper. As soon as all the bugs have fed the paper is pushed back to the bottom of the tube. The great advantage of using these tubes is that the observer can see exactly how the bug feeds, copulates and lays its eggs. They can be carried in the pockets without the danger of the bugs escaping, provided they are properly plugged with cotton wool.

Cimex columbarius, Jenyns. This species is smaller and more orbicular than *lectularius*, which, however, it closely resembles, especially in colouration. Its antennae are shorter and the joints not quite so slender; the difference in length between the third and fourth joints is not so great as in *lectularius*. The prothorax is less hollowed out in front, and the anterior angles less produced; the sides are much less reflexed. The abdomen is much rounder than in *lectularius*; its greatest breadth is just behind the middle.

This species is common in Europe in the nests and coops of pigeons; in the United States it has been recorded by Girault from a chicken house, in a large fowl yard at Anacostia, D.C. It is probably more widely distributed than the records would lead one to suppose.

Cimex hirundinis, Jenyns. This species is smaller than either *columbarius* or *lectularius*, and in general form differs from both species. Its antennae are comparatively short, and the third joint scarcely if at all longer than the fourth; according to Jenyns the eyes are not so prominent as in the other two species. The prothorax is much less hollowed out in front, the anterior angles are only a little produced towards the eyes, and the sides slightly reflexed and more like those of *rotundatus*. The elytra are less coarsely punctured. The abdomen is not so broad, and is more rounded at the apex; the sides are regularly curved. The whole insect is more pubescent, and its colour is ferruginous inclining to testaceous, and darker than *lectularius*. This species is common in Europe in the nests of *Hirundinis urbicae*.

Cimex pipistrelli, Jenyns. This species is closely allied to *rotundatus*. The antennae are intermediate in length between those of *lectularius* and *columbarius*; the third joint is longer than the fourth. The eyes are prominent. The prothorax is moderately excavated in front and the sides only very slightly reflexed. The abdomen is narrower than in either *lectularius* or *columbarius*, and is much more attenuated posteriorly than in *rotundatus*; the greatest breadth is just in front of the middle of the abdomen. The whole insect is very pubescent and coarsely punctated. Its colour is like that of *rotundatus*, dark ferruginous ochre. This species has been recorded from the common pipistrelle in England and from a bat in South Africa; it has been taken from *Scotophilus kuhli* in South India.

Cimex boueti, Brumpt. This species was found by Bouet in French Guinea, where it is said to suck the blood of man; Brumpt figures both sexes in his *Precis de Parasitologie*, pp. 563, 564. The prothorax is quadrilateral in shape, the anterior angles hardly if at all produced and the sides not reflexed. The abdomen is ovoid in shape and the elytra are rudimentary; the body is only sparsely covered with hairs. The biology of this species has been described in a recent paper by Joyeux (see Appendix).

GENUS LOXASPIS, ROTHSCHILD

Reflexed margin of pronotum very narrow. Scutellum transversely oblong, produced into a small point in the centre of the hind margin. Elytra transverse, widest towards the suture. Tibia with a pseudo-joint at about four-fifths of the length.

Loxaspis mirandus, Rothschild. This bug has recently been described by Rothschild, as follows:—Head, thorax, elytra, abdomen and legs densely covered with very fine hairs inserted in pits; colour dark brown.

Head (without labrum) one-fifth shorter than the pronotum. Pronotum at apex not sinuate, almost truncate, and of equal width throughout, the sides being slightly incurved; anterior angles slightly produced but not reaching half-way towards the eye; posterior edge also truncate; explanate margin narrow, slightly reflexed and of the same width all round except at the apical angle, where it is very slightly widened. All the tibiae possess a pseudo-joint at about four-fifths of their length. According to Rothschild this is a very distinctive character, and is not known in any other species of the Cimicidae. Length, 4 mm.

This bug was found in a house in Kilindini near Mombasa, and is probably parasitic on the bat *Taphozous hildegardeae*.

Of the other genera of the Cimicidae, *Cacodmus* is found in South Africa, *Oeciacus* in Europe and North America and *Haematosiphon* in Central America; it is not known whether the species belonging to these genera are blood-suckers or not (see Appendix).

FAMILY POLYCTENIDAE, GIGLIOLI

Small (3 mm.) very aberrant bugs closely allied to the Cimicidae. *Head triangular in shape and articulated to the thorax by means of a* *well-marked neck; a row of ctenidia situated along the posterior border of head and an oblique row on the dorsal surface. Labrum well developed. Antennae short, four-jointed and directed backwards. Prothorax elongated and broadest a little behind the centre; anterior angles somewhat prolonged. In addition to a number of small bristles there is a row of three or more long ones on the dorsal surface of the prothorax, and a row of ctenidia along the posterior border. Elytra elongated, somewhat quadrilateral in shape, united in front and separated behind; their posterior borders may or may not be armed with ctenidia. Abdomen ovoid in shape, consisting of eight segments, a row of small bristles on the posterior borders of the dorsal surface of each segment; the bristles on the last three segments are longer. Legs relatively short, tarsi four-jointed in imago and three-jointed in nymph.*

This remarkable family of bugs, of which seven species and nineteen specimens are known, contains the single genus *Polyctenes*, Gigl. They are all parasitic on bats and live deep down in the fur of their hosts, where they may be very easily overlooked. Westwood placed the family Polyctenidae in the order Anoplura, but Waterhouse, who had the opportunity of studying an American species, believed they were true bugs. Still later Speiser examined two new species and was able to confirm Waterhouse's statements, that they are closely allied to the Cimicidae. In the larval stage the ctenidia are present on the head, in the nymphal stage they appear on the elytra, and in the adult stage on the thorax. Speiser gives the following list of species:—

P. molossus, Gigl., from the 'Chinese Molossus,' from Amoy.
P. lyrae, Waterh., from *Megaderma lyra*, from Secunderabad, India.
P. intermedius, Speiser, from *Taphozous perforatus*, from Egypt.
P. talpa, Speiser, from *Megaderma spasma*, from Nias, and from *Cynopterus marginatus* from Trivandrum, South India.
P. spasmae, Waterh., from *Megaderma spasma*, from Java.
P. longiceps, Waterh., from *Molossus abrasus* from Cajabon in Guatemala.
P. fumarius, Westw., from *Molossus rufus* var. *obscurus*, from Jamaica.

INTERNAL ANATOMY OF CIMEX ROTUNDATUS

The *alimentary tract* of the bed bug is simple in form and of moderate length. It consists of a sucking pump in the head, comparable to that of the Diptera, an oesophagus, a mid-gut, which makes up by far the greater part of the tract, a hind-gut with a rectum, and the Malpighian tubes.

The alimentary canal

The pharynx or sucking pump

The sucking apparatus, or *pharynx*, consists of two plates superimposed upon one another in the transverse plane, the dorsal plate having a series of muscles by means of which it can be withdrawn from the ventral one. It lies in the ventral portion of the head, about the level of the bases of the antennae. Each plate is heart-shaped, with its narrow end directed forwards and rounded off (Plate LXIV, fig. 7). The muscles which withdraw the dorsal plate from the ventral one, and so create the necessary negative pressure, arise from the dorsal and lateral walls of the head, and pass obliquely inwards to the upper surface; they are inserted into the lateral areas of the plate, not into the middle line as is so frequently the case. There is no sphincter muscle, the flow of blood being apparently determined by a peristaltic method of contraction.

The pharynx does not extend quite to the point at which the mandibles converge to form the food channel. The interval between the two is occupied by a shallow chamber with membraneous walls, which may be termed the buccal cavity; this is supported at the sides by a chitinous arch produced forwards from the plates of the pharynx. It is not provided with a musculature. A considerable portion of the ventral surface in this region is occupied by the salivary pump, the distal end of which is split up into a number of fine chitinous processes, which appear to guard the opening into the buccal cavity on each side. The exact means by which the food canal in the proboscis is connected with the pharynx has not been made out. They have no chitinous continuity.

The *oesophagus* is an extremely thin and delicate tube, commencing at the posterior end of the pharynx, and passing through the brain and neck to join the mid-gut at the posterior end of the thorax. Its wall contains a good deal of muscular tissue, and can be seen to be in active peristalsis during the act of feeding, if young bugs with a transparent integument are examined.

The mid-gut

The *mid-gut* (Plate LXIV, fig. 1) comprises almost the whole of the rest of the tract. It may be divided into two portions, which probably correspond to the cardia and the proximal intestine in the higher Diptera. The cardia, or anterior part, is the widest, and runs straight backwards to the posterior end of the body; it is constricted in seven or eight places in the circular direction, the constrictions giving it a saccular appearance, and is separated from

PLATE LXIV

Figure 1. The alimentary tract of *Cimex rotundatus*. oes. oesophagus. sl.g′., sl.g″., the cardiac glands. cd., the cardia, or anterior part of the mid-gut. v., valve-like constriction at the posterior end of the cardia. mg., mid-gut. mp.t., Malpighian tubes. Note their low insertion into the gut. rt., rectum. × 10.

Figure 2. The tubular salivary gland of Landois, after Landois.

Figure 3. The branched salivary gland of Landois, after Landois.

Figure 4. The chitinous structures at the distal end of the head of *Cimex rotundatus*, showing the salivary valve, sl.v., into which opens the salivary duct, sl.d. ch.a., a chitinous ridge produced backwards to the ventral wall. r., the rod of the pump, acting like a piston rod, by means of the muscles, mu. mb., membraneous area anterior to the pharynx, corresponding to the buccal cavity. ph., the pharynx. × 450.

Figure 5. The pharynx or sucking pump of *Conorhinus rubrofasciatus*, seen from the side, from a cleared preparation. h.c., chitin of the head capsule. lr., labrum. oes., oesophagus, emerging from the posterior end of the pump. × 64.

Figure 6. The salivary pump of *Conorhinus*, seen from the dorsal aspect in a cleared preparation. sl.a., salivary aperture. ch.r., chitinous ridge lying ventral to the pharynx and partly fused with it, which serves for the attachment of the muscles of the pump. sl.d., the point of entry of the salivary duct into the valve. r., the piston rod of the valve. mu., the muscles which draw out the plunger of the pump. × 320.

Figure 7. The pharynx and salivary apparatus of *Cimex rotundatus*. md., mandible. md.b., its basal enlargement. sl.g′., the reniform salivary gland. Other letters as above. Only a part of the oesophagus is shown. × 130.

Figure 8. One side of the terminal filament of the salivary valve of *Cimex rotundatus*, showing the serrated edge on the dorsal aspect.

Figure 9. The same, seen from the ventral aspect.

PLATE . LXIV.

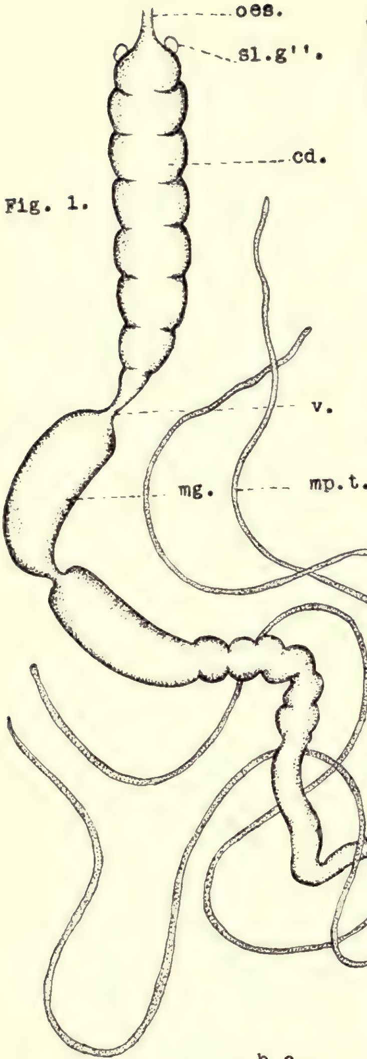

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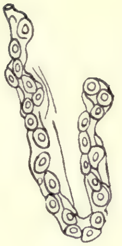
Fig. 1.



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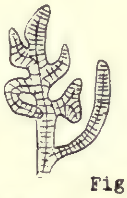

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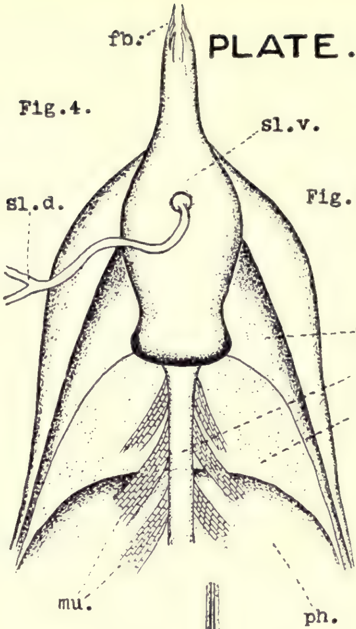
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Fig.4.

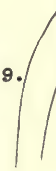

Fig.9.

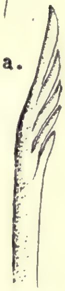

Fig.8.

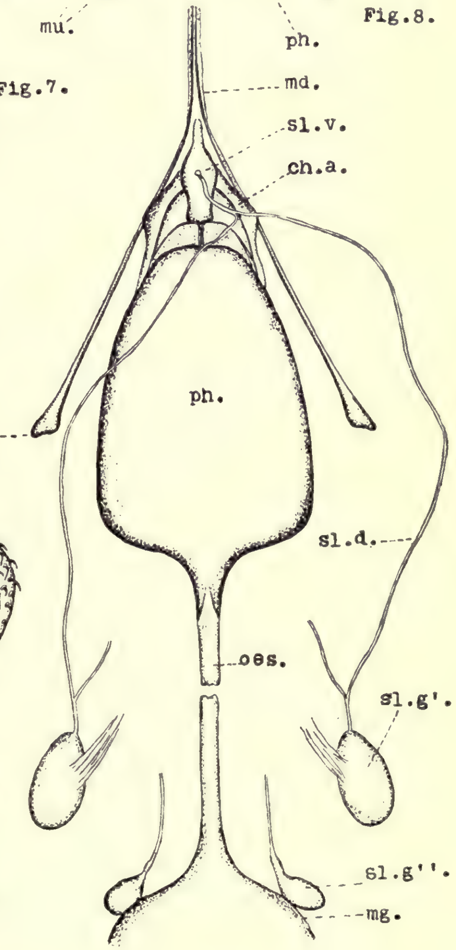
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Fig.7.

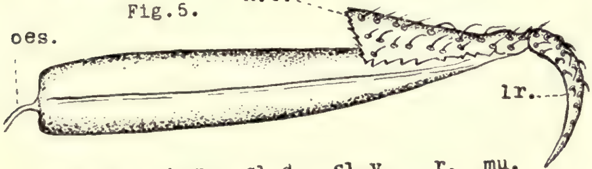

Fig.5.

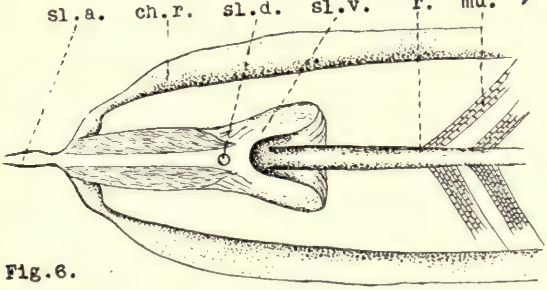
sl.a.
ch.r.
sl.d.
sl.v.
r.
mu.

Fig.6.

the posterior portion by a well-marked constriction which is almost constant in position. In the fasting condition this part of the gut is usually filled with bubbles of gas, and contains also a few granules of black pigment. When the bug feeds it is this part which receives the blood, and it is to the great distension of its lumen that the rotundity of a fully gorged specimen is due.

The hind-gut

The posterior part of the gut, or the proximal intestine, is roughly about twice as long as the cardia, and is coiled up in the posterior part of the abdomen. Its diameter is very variable and its contour irregular, as the tube is divided up into a number of compartments, which are quite inconstant in position, by contractions of isolated bands of circular muscles fibres. It never contains fresh blood, which is retained in the cardia by the sphincter muscle during the first part of digestion, but always contains a large amount of a fluid with a heavy suspension of brownish black granules—the remains of the last meal.

The cells of the wall of the mid-gut are of the usual secreting type. In the anterior portion they are columnar in the resting condition, and flattened when the gut is filled with blood, while in the posterior part they are cubical. In both situations, however, they exhibit great variation and irregularity in form, on account of the changes which occur in the secretion and excretion of the digestive juices. No peritrophic membrane has been described, though it may exist.

The *rectum* is relatively large, and is pear-shaped. It always contains a quantity of the same black granule-containing fluid which is found in the portions of gut anterior to it, and is often very much distended. It has a chitinous lining, as in the Diptera. There are no rectal papillae.

The *Malpighian* tubes are four in number, and are inserted separately into the gut at the anterior end of the rectum, their low insertion being a remarkable feature. They are of the usual structure, and have crenulated margins as seen in the proximal portions of the tubes in *Philaematomyia.* The tubes are of uniform diameter and appearance throughout.

The salivary apparatus

The *salivary apparatus* of the bed bug consists of at least two pairs of glands with extremely long and delicate ducts, and a salivary pump in the head. The two pairs of glands may be distinguished for the sake of convenience as the ovoid and cardiac glands respectively. The *ovoid glands* (Plate LXIV, fig. 7) lie at each side of the anterior end of the stomach, slightly anterior to the junction between the metathorax and the first abdominal segment. When distended with secretion they are ovoid or pear-shaped, the broad end being directed forwards; after the discharge of their contents they lose their tense and rounded appearance, and become a little elongated. The wall consists of a single layer of flattened cells, with some fine muscle fibres. They lie free in the haematocoele, and when the thorax and abdomen are drawn apart, as in the method of dissection to be described presently, the two glands generally slip out through the rupture in the body wall. A fine duct with a ringed chitinous intima, like that found in the salivary ducts in the Diptera, emerges from the broader anterior end, and passes forwards for a distance less than the length of the gland; it then divides, the two resultant ducts being, as Landois pointed out, only half the thickness of the common duct, suggesting that saliva flows through both channels. One of these two ducts can be traced without much difficulty through the neck to the salivary pump in the head, near which it unites with its fellow of the opposite side to enter the pump in the middle of its ventral surface. The other duct has not been followed to its destination by the present writers. Landois states that it passes first forwards, then bends again backwards towards the abdomen, reaching the anterior region of the stomach, and finally bends again forwards, to open into the stomach near its junction with the oesophagus—a remarkable mode of termination for a salivary duct.

These glands are held in position by an arrangement of fine fibres which are inserted, according to Landois, in the integument of the head. The fibres arise from the whole surface of the gland, and are collected together to form a fine cord at the inner side of the common duct at its origin from the gland. The suspensory cord is very easily ruptured if the head is pulled away from the thorax, and has not nearly as much resistance as the duct, a point which throws some doubt on the function assigned to it. It seems more probable that the muscle fibres in the cord, spread out as they are over the whole surface of the gland, serve to compress it when the saliva is to be ejected.

The *cardiac glands* (Plate LXIV, figs. 1 and 7, s.l. g.) lie on either side of the anterior end of the stomach, and are separated from one another by the oesophagus. They are round or oval in shape, and are attached to the wall of the gut by fibrous bands. In structure they resemble the pair just described. A fine duct emerges from the anterior end, and passes forwards to the head. Landois states that it enters the 'crop' (pharynx) but the present writers have not succeeded either in tracing the duct into the head or in finding any channel entering the crop except the oesophagus.

The *tubular salivary glands* (Plate LXIV, fig. 2), described by Landois, lie in the neighbourhood of the cardiac glands. Each consists of a fine tube bent upon itself, the wall being formed of a single layer of small cells with some muscular tissue. According to their discoverer they are best recognized by their rythmical contractions. They are said to open into the commencement of the crop. The *branched salivary gland* of Landois (fig. 3) is even more minute and difficult to find than the preceding. It consists of short branched tubules arising from a common stem, which opens into the oesophagus.*

Landois suggested that the secretion of the salivary glands passes partly into the wound at the time of feeding, and partly into the alimentary tract during the intervals. This is not in accordance with what one finds in other blood-sucking insects. Possibly those glands which open into the alimentary tract posterior to the mouth have some function other than the elaboration of saliva.

The salivary pump

The *salivary pump* or *valve* (Plate LXIV, fig. 4) bears a striking resemblance to that which has been described in the mosquito. It lies anterior and ventral to the pharynx, and is attached to the ventral wall and the supporting arch of the membraneous chamber which has been referred to as the buccal cavity. It consists of a spindle-shaped or vase-like cup of chitin, somewhat elongated in front, and with its narrow end directed to the point at which the two mandibles come in contact with one another. The broad posterior end is closed in by a membrane, in the middle of which there is inserted a short rod of chitin, which passes upwards a little distance below the ventral wall of the pharynx. A number of bands of muscles fibre pass obliquely from the ventral surface of the pharynx to the rod, contraction of these pulling the rod, and therefore the membrane, away from the cup, and thus creating a negative pressure within its cavity. The salivary duct, formed by the union of the ducts of the two sides, opens into the middle of the ventral surface of the cup, and the negative pressure will therefore result in drawing the saliva from the glands into the pump. The ducts are lined throughout with a ringed chitinous intima like that of a trachea, which will effectually prevent occlusion. Presumably there is some valve which prevents ingress of blood into the pump when it is in action. The passage of the saliva from the pump is best accounted for, as suggested by Nuttall and Shipley in the case of the mosquito, by the elastic recoil of the membrane. There are no muscles which could force the piston rod forwards.

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* Neither of these glands has been seen by the writers.

The salivary pump is by no means easy to find or to dissect out, and was not described by Landois. It is best seen in longitudinal sections.

Reproductive system (Plate LXV)

The *organs of reproduction* in the bed bug present many very remarkable features, both as regards their structure and function. The whole process of reproduction is carried on in a highly abnormal manner, for the sperms, instead of being destined solely for the fertilization of the eggs, probably also contribute to the nourishment of the pregnant female. The subject is very obscure, and must remain so until a comprehensive study of the development of the parts is undertaken; the following account is offered with reserve, as an indication of the nature of the problem rather than an explanation.

The male organs

The male organs (Plate LXV, fig. 1) conform generally to the ordinary type, though they differ markedly in appearance from those so far described. The *testes* are pyramidal bodies, the broad end of each being directed outwards and forwards, the narrow apex leading to the *vas deferens*. Each testis is made up of seven wedge-shaped lobes, the narrow end of each of which reaches to the commencement of the vas, while the broad ends lie side by side on the anterior surface of the organ. The lobes are separated from one another by delicate fibrous septa, which extend to the external capsule of the gland, producing indentations on the surface where they fuse with it. At the posterior end of each testis there is a small isolated spherical lobe, closely attached to the commencement of the vas, without a stalk. This is not figured or described by Landois in *Cimex lectularius*, but is of constant occurrence in *rotundatus*. It may be an accessory gland, or a degraded lobe of the testis. The *vas deferens* is relatively short and stout, being not more than twice the length of the testis. It is narrow in the upper part, but widens out in a spindle-shaped manner towards its lower end. In the fresh condition it has a greenish yellow colour, and is translucent. According to Landois it is frequently distended with sperms.

The *accessory glands* (Plate LXV, fig. 2) are situated at the lower end of the vasa. On each side there is a small branched gland consisting of a number of tubules of varying length but of uniform diameter, irregularly arranged. This opens by a short duct into a pear-shaped chamber, which probably acts as a reservoir for the secretion of the gland. It is placed in close apposition to the end of the vas of its

PLATE . LXV.

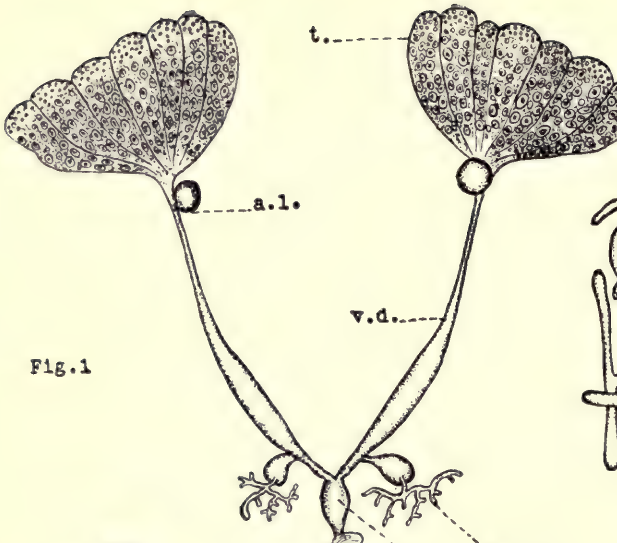
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Fig.1

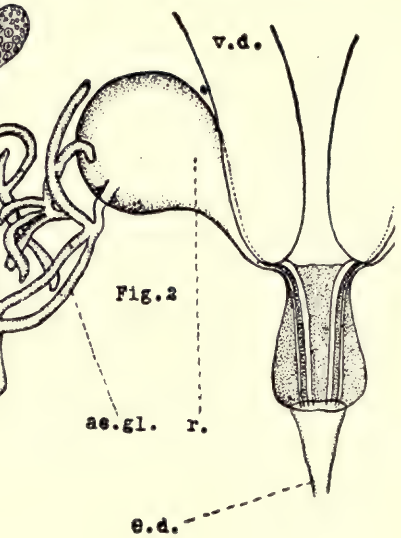
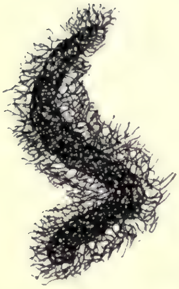


Fig.2



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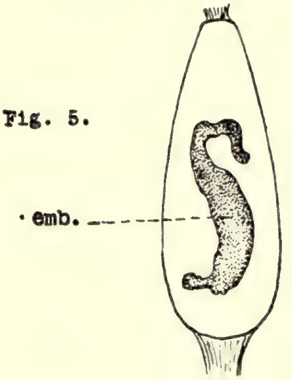

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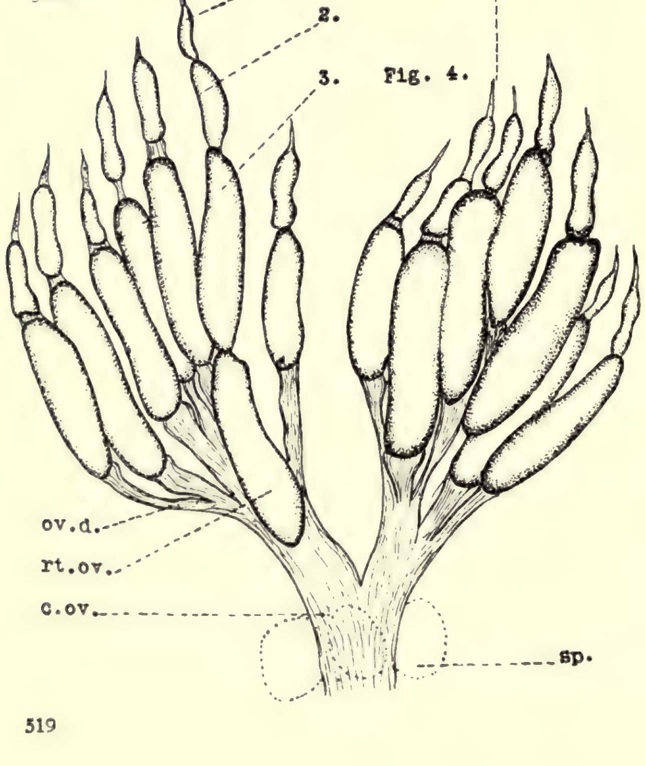
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Fig. 4.

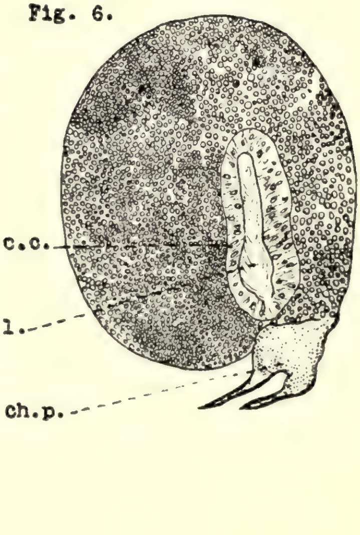

Fig. 6.

PLATE LXV

Figure 1. The male reproductive organs of *Cimex rotundatus*. t., the testes, each consisting of seven lobes. a.l., accessory lobe of the testis. v.d., vas deferens. ac.gl., accessory gland. r.sem., the seminal vesicle. p., the penis. × 10.

Figure 2. The accessory glands of the male reproductive system of *Cimex rotundatus*, more highly magnified. r., reservoir of the accessory gland. e.d., ejaculatory duct. Other letters as above. × 60.

Figure 3. A mass of sperms from the abdominal cavity of the female *Cimex rotundatus*. × 66.

Figure 4. The ovaries of *Cimex rotundatus*. 1, 2, 3., the first, second, and third follicles of the ovarian tube. g., the apical thread and germarium. ov.d., the oviduct of one of the follicular tubes; those of each side unite to form a common duct, the common ducts of the two sides uniting to form a common oviduct, c.ov. sp., the positions usually occupied by masses of sperms, which become adherent to the wall of the common oviduct and simulate spermathecae. rt.ov., a ripe ovum retained in ovary. × 20.

Figure 5. An ovum of *Cimex rotundatus*, showing the formation of the embryo within it while still contained in the ovarian tube. × 35.

Figure 6. A section through the middle of Berlese's organ. The organ appears to consist of a mass of small round cells, within which there is a chitinous channel continuous with the plate on which the opening is situated. l., the lumen of the chitinous duct. c.c., the cylindrical cells around it. ch.p., the chitinous plate in which the orifice is situated. × 40.

This represents only one phase of the organ. In other series of sections very different appearances may be seen.

own side, so that only the rounded distal portion is visible in most preparations. At the lower end of the vasa there is a short but wide chamber in the middle line, which communicates below with the penis; neither the vasa nor the ducts of the accessory glands, however, open directly into this chamber, but lead into it by fine ducts, four of which can be traced within the wall in suitably stained preparations. They have not been followed to their ultimate terminations.

The female organs

The reproductive organs of the female present an extraordinary condition of affairs. Unfortunately the authors, in discussing this problem, are at a great disadvantage in not having been able to consult the original papers in which the matter has been dealt with by Berlese and Carazzi; their own observations, moreover, are not in accord with the account given in Berlese's book, a fact which makes it still more undesirable to make definite statements without a much more exhaustive study than could be undertaken in the time available. A brief description of the anatomy of the parts, with an account of Berlese's views as given in his book, and some original observations, must suffice for the present. It should be noted that Berlese's account refers to *Cimex lectularius*, not *rotundatus*.

The *ovaries* (Plate LXV, fig. 4) do not present any special features. Each consists of seven ovarioles, each ovariole having an independent ovarian tube, those of each side uniting to form a single channel, which in turn joins its fellow of the opposite side to form a common oviduct. This leads directly to the genital aperture. Berlese describes and figures two spermathecae, but there are certainly none in *rotundatus*, though, as will be seen later, there are accumulations of sperms, in the position in which one would expect to find spermathecae, which might easily be mistaken for them. The separate ovarian tubes show, as a rule, only two follicles each. The lowest one contains a ripe or nearly ripe egg, having the same appearance as the egg when laid, the slight bend in the length and the flattened upper or cephalic end being clearly discernable. It is unusual to find all the eggs in the lowest row of follicles at the same stage of development, the variation in size being a striking feature when one compares the ovary with that in the Diptera. Many eggs (fig. 5) contain well developed embryos, in which the pigmented eyes can be clearly seen, and in one case an embryo was found so far advanced that it had actually thrust off the cap at the end of the egg, although still contained in its follicle. Mature eggs are often found in the lower part of the ovarian tube, presumably left behind at the last act of oviposition, so that one tube may contain two mature ova.

The second follicle is usually distinctly separated from the first by a constriction, and is elongate and slightly narrowed in its middle. The lower half contains the nucleus of the ovum, with a considerable amount of granular material, while in the upper half there is a mass of nutritive cells, many of which are cylindrical and directed axially towards the growing ovum. At the upper end of the second follicle there is a small cluster of minute undifferentiated cells, the *germarium*, from which future follicles will be developed; from the upper end of this the usual apical thread passes forwards to the dorsal region of the anterior end of the abdomen.

The organ of Berlese

The *organ of Berlese* (Plate LXV, fig. 6) is a small round body of a dull white colour, lying on the right side of the ventral region of the abdomen, immediately above the incision in the ventral margin of the fourth segment. It is closely adherent to the integument, but is free from the internal organs, the scanty supply of tracheae which it receives being insufficient to bind it down to them. No duct can be found running between it and the ovaries, though they are supplied with tracheae from a common stem, a branch of which might easily be mistaken for a duct. At the place at which it is attached to the integument there is a small oval plate of chitin in the membrane between the fourth and fifth sternites, and in the centre of this is a minute aperture, guarded by extremely fine spines. From this aperture a chitinous duct leads into the interior of the organ. The substance of the organ is composed of a mass of round cells arranged around a small central space, the extent of the lumen varying a good deal in different conditions. The whole structure is surrounded by a very thin but definite capsule. No aperture leading from the chitinous duct to the central space has been found, but there is strong reason to believe that it exists. The cells immediately surrounding the duct are smaller and more cylindrical than those which make up the rest of the organ, and have different staining reactions. In one of Berlese's figures the central portion surrounding the duct is referred to as the *organ of Ribaga*.

The appearance of the organ on section differs very greatly in different cases, from causes which cannot as yet be explained. The cells may be more or less uniform in arrangement and in shape throughout the organ, or they may be more densely packed and smaller in one part than in another; in some parts they may be degenerated and apparently replaced by a finely granular mass, or practically all the cells may be enlarged and vacuolated. Since no satisfactory explanation of these appearances can be given at present it is hardly worth while to describe them in further detail.

To come now to the explanation of the function of this organ, given by Berlese. It has already been indicated that he has described and figured a pair of spermathecae in *Cimex lectularius*, and it is to be assumed from this and from other points in his account that he believed copulation to take place in the ordinary way, the male organ being introduced into the genital aperture of the female. He states that, in the spermatheca of the right side, which is the larger one of the two, there is a minute pore, through which the sperms can pass out into the abdominal cavity. They then make their way to the organ of Berlese, within which they are destroyed and used up as food material during the period when the female has special need of such for the maturation of the eggs. Some of the sperms pass to the ova and fertilize them in the ordinary manner. The greater part of the sperms received from the male, therefore, are used up by the female as food material, the phenomenon being termed by Berlese 'hypergamesis'. Another and rather different instance of the same process had previously been described by the same author in *Scutelleridi*.

Copulation in Cimex

Such a state of affairs would be remarkable enough, if that were all, and Berlese's explanation a complete one, but there is strong reason to believe that this is far from being the case. The strongest evidence against it is the method of copulation of the bed bug. Most bugs when copulating attach themselves to one another by their posterior ends, and remain attached for some time; plant bugs may be frequently seen fastened together in this manner. The bed bug, however, does not do this, and nothing suggesting this method of copulation has ever been seen by the senior author in a very large experience of breeding both *rotundatus* and *lectularius*. On the other hand, copulation, or what looks extremely like it, is carried on in another fashion quite frequently; it is usually observed immediately after feeding, but this may, of course, be because it is at that time that bugs kept for experimental purposes are most under observation. The male bug approaches the female from behind, and, with a sudden movement, places his body obliquely across hers, remains in that position for a few seconds, and leaves as rapidly. From the position of the male it is impossible for his penis to reach the genital opening of the female, whereas he is placed precisely as one would expect if his intention were to introduce it into the opening of Berlese's organ, for he is invariably on the right side of the female, and just sufficiently far forwards to bring his posterior segments on a level with the opening. The operation is carried out so quickly that it is not possible to obtain final proof by killing the pair *in copulô,* but repeated observations on many separate occasions have left no doubt in the minds of the writers that the male organ is actually introduced into the opening of Berlese's organ.

Further evidence is afforded by an examination of the organ immediately after copulation of this sort has been actually observed. In every case the lumen has been found distended with a mass of sperms, which, when dissected out in saline, show active movements of the usual kind. Sections of Berlese's organ removed immediately after copulation have also been made, and confirmed the result of dissection. Under no other conditions has the same mass of active sperms been found inside the organ.

Berlese states that the spermatozoa are ingested and destroyed by the cells of the organ, and gives figures showing them within the cells ; this has not been confirmed so far, but bodies which may be the products of the digestion of the sperms have been frequently observed, especially in those cases in which all the cells of the organ are enlarged and vacuolated. As was stated above, no aperture or duct connecting the ovaries or the abdominal cavity with the organ has been found, and consequently no explanation as to how the sperms leave the lumen is forthcoming. In one case, however, the mass of sperms was seen to be very near the periphery of the organ, as if it were pushing its way through *en masse.* That the sperms do actually leave the organ is quite certain, for they are to be found in little clumps (Plate LXV, fig. 3) within the abdominal cavity in almost all mature female bugs, lying free or attached to the viscera ; those at the edge of the clump always show active lashing movements. Berlese appears to have noted the presence of these masses, which are often large enough to be visible to the naked eye, and regarded them as spermatozoa on their way from the spermatheca to the organ destined for their destruction, whereas, if the phenomenon described above is really copulation, the sperms are travelling in the reverse direction.

These masses of sperms are very characteristic in appearance, and once the eye becomes accustomed to them they can be readily distinguished from fat body. They are to be found all over the abdominal cavity, but in the largest number around the common oviduct, to which they become adherent in larger clumps, often very closely simulating small sacs which might be taken for spermathecae (fig. 4) ; in fact, the authors confess that they at first regarded them as such, until their attention was arrested by the fact that they could not be stained in the ordinary manner, and that the outline was always hazy. It was only by very deep staining with haematoxylin, and subsequently by cutting a series of sections, that their true nature was revealed.

With regard to the ultimate fate of the sperms, little can be said at present. The fact that they accumulate around the common oviduct suggests that they are on their way to the ova, and should this be their ultimate destination it would possibly have some connection with the high degree of development which the embryo may attain while still in the ovary. That they are able to pass at will through other tissues seems very likely, in view of their great motility and of the fact that no aperture can be found in either the wall of Berlese's organ or the oviduct. On at least two occasions active spermatozoa have been seen within the lumen of the gut while it was still unruptured.

As to the true nature and origin of Berlese's organ and its opening, one hesitates to speak : if a suggestion were to be offered, it would be that they represent a survival of paired and segmental genital organs and pores of a remote ancestor.

The stink apparatus

The bed bug, like many of its non-biting allies, is provided with an apparatus for the production and emission of an evil smelling fluid, the object of which is to protect the insect from its enemies. The apparatus consists of a stink gland and reservoirs, and lies in the ventral and posterior part of the thoracic cavity, opening to the exterior at the border of the metasternum. An excellent account of these structures is given by Landois. The stink gland is a small kidney-shaped body, consisting of a number of pear-shaped cells, which are arranged with their broad ends next the wall, their narrow ends directed to the lumen, into which they pour their secretion. The secretion itself is a highly refractile, colourless, and exceedingly malodourous oil. At the point corresponding to the hilum of the kidney there is an opening which leads from the gland to the reservoir. The two reservoirs are elongate and spindle-shaped blind sacs, joined together at their lower ends. When filled with secretion their walls are smooth and taut, but when the oil has been expelled they become wrinkled ; the walls are exceedingly thin. The efferent duct is a strongly chitinized funnel-shaped structure, which leads from the united outer ends of the reservoirs to the exterior, opening between the last pair of legs at the hinder border of the metasternum. The external opening is too small to be seen from the outside.

Although there is no mechanism evident by which the secretion can be expelled, there is no doubt that it is under control, and can be discharged at will when the insect is annoyed or attacked by an enemy. The scent is much more readily perceived by some people than by others, and that of *lectularius* appears to be more powerful than that of *rotundatus.*

DISSECTION OF CIMEX

The following method of dissecting the bed bug has been found satisfactory. After having killed the insect by placing it in a tube plugged with cotton wool containing a few drops of chloroform, it is taken up with a pair of fine forceps and the legs are pulled off. In removing the fore legs care should be taken not to damage the prothorax. The elytra are next removed by raising them with the forceps and gently twisting them off from their joints at the angles of the mesothorax. The bug is now placed on a slide in a drop of saline solution under a dissecting microscope, with its dorsal surface uppermost, its head directed towards the dissector. With the left hand a fine needle is inserted into the right side of the prothorax, and with another needle in the right hand the joint between the prothorax and mesothorax is separated. By gently drawing on the needle in the left hand and by exerting pressure on the dorsal surface of the abdomen with the other needle, the prothorax is separated from the mesothorax, and the oesophagus, mid-gut and the remaining parts of the intestinal tract are drawn out; any portion can then be isolated from the rest. The ovoid salivary glands, which lie free in the haematocoele, are readily recognized by their slightly yellowish colour. The cardiac glands lie on each side of the anterior end of the mid-gut. The oesophagus can be followed into the head by slowly picking away the prothorax, and the sucking pump or pharynx can be displayed by breaking up the head; this is accomplished by first passing a needle through both eyes and then cutting through the sides of the head and reflecting off the dorsal wall; the pharynx lies on the ventral side. The hind-gut is best dissected out by nicking the last abdominal segment and slowly separating it from the rest of the abdomen; great care should be taken not to rupture the rectum as it is nearly always full of a black fluid which spoils the preparation. The internal genital organs usually come away together with the rectum. The best way to dissect out these organs is to place the bug in the dissecting trough and to fix it by passing a pin through each side of the prothorax; the abdominal segments are now nicked along their borders and bit by bit each tergite is reflected off. In this way all the organs, especially that of Berlese, are well displayed.

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CHAPTER VII

THE ORDER ANOPLURA: LICE

THE Anoplura constitute a small order of blood-sucking insects which are entirely parasitic on mammals. Both in their structure and life history they exhibit in a high degree those features which are commonly associated with the parasitic habit, and form in this respect an interesting comparison with the less specialized fleas. The body is compressed in the dorso-ventral direction, so as to oppose as little resistance as possible when the insect moves about among the hairs or fur of the host, and is enclosed in a tough and leathery integument which is not easily ruptured. They are wingless, and have the legs very strongly developed; the feet are armed with powerful claws to enable the parasite to retain its hold. The metamorphosis is incomplete; the young resemble the adults, and the eggs are laid among the hairs of the host, to which they are attached by an adhesive substance secreted by the female, so that the entire life cycle is passed upon one animal. Further, the separate species are usually limited to a particular species of host, and cannot thrive on any other.

The relationship of the Anoplura to other groups of insects has long been in dispute. They have been placed near the Mallophaga or bird lice,* which they resemble very closely in body form and general appearance, but from which they are sharply distinguished by the structure of the mouth parts; the Mallophaga are provided with a pair of strong mandibles, easily recognized under the microscope on account of their dark pigmentation, and live on solid food, while the true lice have a complex sucking and piercing apparatus, and live exclusively on blood. Enderlein regards the Anoplura as closely allied to the Rhynchota, mainly on account of a similarity which, it is claimed, exists between the mouth parts of the two groups. The mouth apparatus of the louse is, however, very complex and difficult to study, and as no common agreement has as yet been reached with regard to the homology, or even the mechanism, of the parts, too much stress should not be laid on such a criterion; one has, moreover, to bear in mind that in the Diptera there are many species which are confirmed blood-suckers, but are nevertheless very closely allied to forms which have no biting apparatus at all. The Mallophaga are already parasitic, and as their mouth parts are arranged on the same general plan as that of the rest of the Arthropoda, and have therefore the same potentialities for adaptation to the blood-sucking habit, a common origin for them and for the Anoplura would be in no sense remarkable. For our present purpose it is sufficient to regard the Anoplura as a fairly well-defined order, without going too closely into the question of their affinities.

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* A few Mallophaga occur on mammals.

The species of lice which infest human beings have long been known to be associated with an uncleanly habit of person, an association which is probably the origin of the feelings of repugnance to which they give rise among civilized people. Their prevalence, in fact, may be taken as an indication of the personal cleanliness of the inhabitants of a locality; in Europe they are much less commonly met with now than appears to be have been the case in the past, while in some parts of the tropics a considerable proportion of the inhabitants harbour them. There is never the slightest difficulty in obtaining them in large numbers in Madras.

Relation to disease

The connection between the presence of lice and personal filth has often led to the suspicion of some causal relationship between them and diseases, such as typhus and relapsing fever, which occur especially in uncleanly surroundings and in times of famine. In epidemics of these diseases it is found that it is always the poorest and least cleanly section of the community which suffers most, and indeed it is only when they are brought specially into contact with such people that persons of ordinary habits become affected. Experimental evidence in confirmation of the observed relations has been produced within recent years. Nicolle, working in Algeria, and Ricketts and Wilder, in Mexico, have succeeded in infecting monkeys with typhus fever by means of the bites of lice taken from the bodies of persons suffering from the disease. The latter observers conclude that although the bug and the flea are also under suspicion, all the epidemiological evidence points to the louse as the transmitter; there is a possibility that the infection may be hereditary in the louse.

With regard to relapsing or recurrent fever, the louse may be said to be now definitely incriminated as the main, if not the only, carrier of the spirochaete which produces the disease.

PLATE. LXVI.

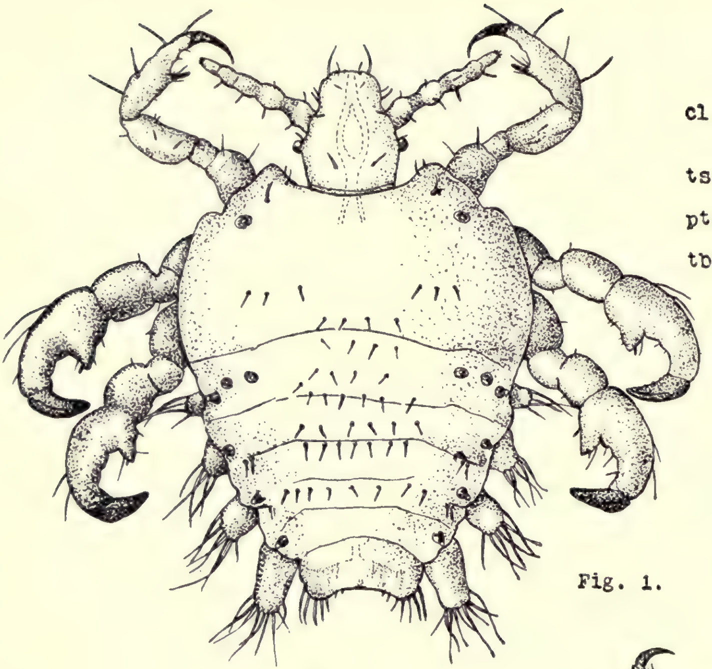

Fig. 1.

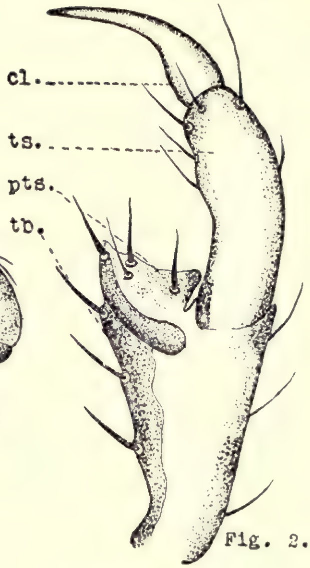

Fig. 2.

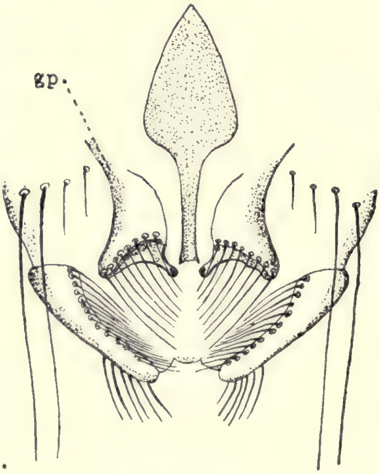

Fig. 3.

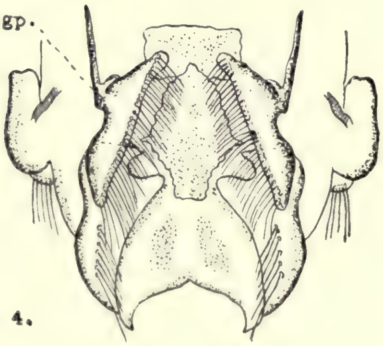

Fig. 4.

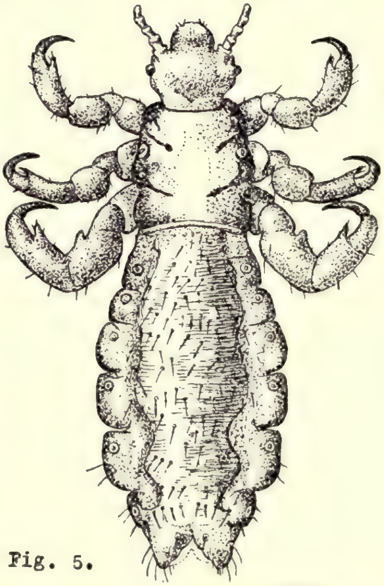

Fig. 5.

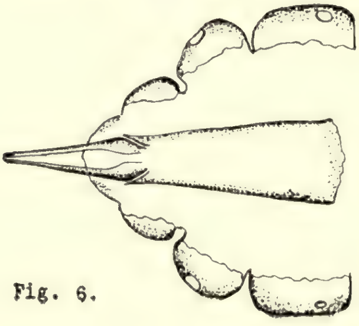

Fig. 6.

PLATE LXVI

Figure 1. *Phthirus pubis*, ♀. × 64.

Figure 2. The tibia and tarsus of the hind leg of *Haematopinus tuberculatus*. cl., claw. ts., tarsus. pts., pretarsal sclerite. tb., tibia. × 80.

Figure 3. Ventral surface of the posterior end of abdomen of *H.* (*Linognathus*) *vituli*, ♀. gp., gonopodes.

Figure 4. The same of *Haematopinus tuberculatus*.

Figure 5. *Pediculus capitis*, de Geer, ♀. × 35.

Figure 6. Outline of the posterior end of the abdomen of *Pediculus vestimenti*, ♂, to show the penis. Compare with the previous figure.

Mackie, working in India in 1907, showed the close relations between the prevalence of lice and the incidence of the disease, and found spirochaetes in lice taken from infected persons. In the following year Ed. Sergeant and Foley, working in Algeria, succeeded in transmitting the disease to monkeys by the inoculation of the body juices of infected lice. Many other observers have noted and recorded the close relations existing between the presence of a large number of lice and infection by the spirochaete, though until the present year the exact method of transmission was not known. Nicolle, Blaizot, and Conseil, however, have recently published a series of observations and experiments, made during the course of an epidemic in Tunis, which go far to clear up the question. They confirmed the close association of lice and the disease, but failed after a large number of experiments to transmit it either to man or to monkeys by means of the bite of the insect; they found, however, that the spirochaetes were not present in the alimentary tract of the louse, but were confined to the body cavity. By rubbing the debris from pounded lice into an abrasion of the skin they were, in two experiments, able to produce the disease in man. They have also produced some evidence which indicates that the offspring of an infected female may be infective.

Several cases are known in which lice act as the invertebrate hosts of blood parasites of mammals. *Haemogregarina gerbilli*, from the jumping rat, *Gerbillus indicus*, was shown by Christophers to pass a part of its life cycle in *Haematopinus stephensi*; the vermicules of *H. funambuli* were seen in a louse from the Indian palm squirrel by Patton. As regards natural parasites, a *Herpetomonas*, first seen by Mackie in India, and subsequently described by Fantham in England as *H. pediculi*, occurs in the alimentary tract of both the body and head lice. It was found by Fantham to occur in circumstances which precluded the possibility of its being a stage in the life history of a vertebrate trypanosome.

EXTERNAL ANATOMY

The body of the louse is flattened dorso-ventrally, is roughly oval in shape, and is distinctly divided into three parts, the head, thorax and abdomen. Of these only the abdomen is distinctly divided into segments.

The *head* is usually more or less conical and pointed, though great differences are found in the several genera in this respect; in *Phthirus*, for instance, it is distinctly four-sided and squat, while in *Haematomyzus* *elephantis* it is greatly elongated. In *Pediculus* and *Haematopinus* the anterior half is produced to a blunt point, while the posterior portion, behind the antennae, is roughly cylindrical. The upper surface is strongly chitinized, and is marked by several sutures, which divide the integument into named portions. A median longitudinal suture runs forwards from the neck for a short distance, and then bifurcates, thus forming a Y with the two limbs directed forwards and outwards to the bases of the antennae. The triangular lateral portions thus marked out make up the *vertex* (' scheitel ' of Enderlein), and the median triangle between the two is the *frons* (' stirn '). The dorsal area in front of the frons is divided, in *Haematopinus* and others, by several transverse sutures, not very distinctly marked, which are taken to represent, from before backwards, the *labrum*, *first* and *second clypeolus*, and the *clypeus*. In *Pediculus* the dorsolateral area at the distal end of the head is specially thickened into a curved plate of chitin, which is considered by Enderlein to be a rudiment of the mandible. The under surface of the head is membraneous, and is often marked by many transverse ridges and furrows. At the distal end the integument is soft and loosely arranged, and shows one or two circular furrows ; it thus permits of a certain amount of evagination of the part, which, as will be seen later, takes place when the insect feeds. The extreme distal end is marked by the presence of a circlet of small chitinous teeth arranged around the mouth orifice. In *Pediculus* there are five such teeth on each side in the adult. As pointed out by Enderlein, the number of teeth differs in different species and in the several instars of the same species. They will be referred to again in connection with the mouth parts and sucking apparatus.

The head

At the posterior border of the head there is a thickened collar of chitin, united to the anterior end of the thorax by a short membraneous neck. Two narrow elongate strips of chitin arise from this in the dorsal middle line, and pass backwards into the thorax. These pieces are well marked in *Pediculus* ; at first they lie side by side with their flattened surfaces dorsal and ventral, but as they pass backwards they turn inwards, and eventually fuse together. Their posterior portions dip below the level of the integument of the dorsal surface, and appear in sections as the two sides of a canal with a narrow and vertical lumen. They are apodemes, serving for the surface of origin of large muscles. Enderlein terms them ' hinterhauptfortsatz '.

The *antennae* are inserted about the middle of the lateral borders. They are simple, consisting of from three to five joints, of which the terminal one is provided with minute sense pits, and are directed outwards and forwards. They are moved freely during life. The number of joints may vary with the stage of development; in *Phthirus*, according to Enderlein, there are only three joints in the larva, while the adult has five.

The *eyes* are always small and inconspicuous, as is usually the case in insects which have become confirmed in a parasitic mode of life, and may be entirely wanting. They are small dome-like elevations, showing a dense black pigment, and are situated on the lateral borders of the head, behind the antennae, sometimes on small forwardly directed processes. The facets can only be seen in sections.

The mouth parts and sucking apparatus

The mouth parts of the louse present an interesting problem in insect morphology, and have been a favourite subject of research from the time of Swammerdam. The obscure nature of the relations of the parts to those in other insects, together with the almost insurmountable technical difficulties which arise owing to the minute size and delicacy of the structures, has led to a considerable amount of confusion in the literature on the subject, both as regards the actual facts of the case and in the nomenclature adopted, on the grounds of supposed homology, by the various workers. It would be out of place here, and it would serve no useful purpose, to enter into a discussion of the views set forth by different observers; the reader who is interested in the subject should consult the paper of Pawlowsky, in which there is a good account of the history of the controversy, and the papers of Enderlein. These two authorities have made the most recent and perhaps the most valuable contributions to the subject, but unfortunately they attacked it from different points and by different methods, and do not adopt the same systems of nomenclature, thereby further confusing the reader. The researches of Enderlein are founded on dissections and on the comparative study of species of several genera, while the paper of Pawlowsky deals solely with the appearance of the parts in sections of *P. vestimenti* alone.

The following account of the mouth parts of *Pediculus vestimenti* has been prepared, with the assistance of the above papers, from sections and dissections. As a matter of convenience, and because the parts are used in classification, the sucking apparatus, or the first part of the alimentary canal, will also be dealt with here.

In the resting position the mouth parts and sucking apparatus of the louse are entirely concealed within the head.* The disposition of the parts, which is quite unlike that in those arthropods previously considered, is best studied in sections of the head.

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* The mouth parts are usually either entirely concealed, or are so arranged as to present no impediment to forward progress, in those insects which have adopted an entirely parasitic habit.

Transverse sections of the head

In a transverse section of the head anterior to the point of insertion of the antennae (Plate LXVII, fig. 2) two separate canals are seen in the middle line, the upper one of which occupies approximately the middle of the section, and is larger and has thicker walls than the other. The upper canal, when traced backwards, is found to become continuous with the oesophagus, which lies, in the posterior part of the head, in its normal position dorsal to the brain, and eventually dips between the supra- and infra-oesophageal ganglia to reach the neck. This canal is evidently a part of the stomodaeum, and from the numerous muscles which are attached to it, as will be seen presently, one can assume that it forms a sucking apparatus of the usual pattern, and that it can be moved in a forward direction. Within the cavity of the lower tube there are several minute chitinous structures cut in section ; these are the mouth parts, probably corresponding to the first maxillae, the labium, and the hypopharynx of other insects. The wall of the canal in which they lie can be traced to the anterior end of the head, where it opens at the same point as the upper canal; posteriorly it terminates at the level of the brain, by fusing with the thickened posterior ends of the mouth parts themselves. The mouth parts are thus enclosed in a 'proboscis sheath', which is in reality nothing more than an invagination of the integument around them.

The sucking apparatus

The apparatus for the ingestion of food therefore consists of two parts, which may be considered separately. The sucking apparatus is easily dissected out of the head in cleared preparations, as its wall is chitinous throughout. When isolated and straightened out (Plate LXXI, fig. 3) it is seen to consist of two distinct chambers, which are connected with one another by a membraneous canal. Anticipating the description of the musculature of these chambers, they may be called the buccal cavity and pharynx respectively, using the terms in the sense in which they have been used in the account of the sucking apparatus of the Diptera. The *buccal cavity*, or first chamber, is elongate, four or five times as long as broad, and is strongly chitinized. The borders are thickened into conspicuous ridges, and at the posterior end these are produced in a backward and outward direction as pointed cornua. The membraneous canal which connects the two chambers is about half the length of the buccal cavity when its natural bend is undone. The *pharynx* is pear-shaped, and leads posteriorly into the oesphagus by its narrow end. The walls of the pharynx are chitinized, but are not so thick as those of the buccal cavity.

At the anterior end of the buccal cavity there is the circlet of minute chitinous teeth previously mentioned as surrounding the mouth opening. These are attached to the membraneous wall of the head, and in the normal resting position are turned inwards and retracted. As will appear later, they can be turned outwards on their bases so as to transfix the skin of the host during the act of feeding.

The structure and mechanism of the sucking apparatus is best studied in series of transverse and longitudinal sections of the head, which reveal a complex musculature. In the distal part of the buccal cavity the lumen is a transverse slit, bounded by dorsal and ventral plates of approximately equal thickness (Plate LXVII, fig. 1). At this point the ventral wall is connected to the dorsal wall of the proboscis sheath by means of a membraneous expansion. The thickness of the walls increases gradually towards the posterior end of the chamber, and at the same time the lateral thickenings become pronounced. They are not mere thickenings of the chitinous wall, as they appear to be when the organ is examined in cleared preparations, but are lateral pockets running on each side of, and slightly dorsal to, the main portion of the lumen; at the extreme posterior end of the buccal cavity they become solid and are slightly separated from the rest of the wall when seen in transverse section.

Musculature of the buccal cavity

The muscles inserted into the buccal cavity are numerous, and are adapted for two purposes, the protraction of the whole structure and the dilation of its lumen. Their precise attachments are very difficult to determine, as they are far too small to be isolated with precision by dissection, and some of them are so short that a slight error in the angle at which a section is taken might give a false impression as to the course. Four pairs can be distinguished. One pair, which consists of four separate strands on each side, lies in the middle line dorsally, and runs directly backwards from the front of the head to the distal end of the cavity (d. pr. in figs. 1 and 2, Plate LXVII). Contraction of this pair must evidently bring about a forward displacement of the buccal cavity. On each side of this pair there is a larger muscle, having only a short course, which runs obliquely inwards from the dorso-lateral angle of the head to the middle part of the dorsal plate of the cavity. None of its fibres pass to the lateral thickenings of the wall, and it must, therefore, be regarded as a dilator, acting, as in the case of *Tabanus*, by the withdrawal of the dorsal plate from the ventral one (d.b.c. in figs. 1 and 2). On the ventral side of this muscle there are two others of considerable size ; the upper one lies immediately external to the lateral thickening of the wall of the buccal cavity, and may, therefore, be termed the lateral protractor (1.pr. as above), while the other is ventral and slightly internal to the thickening, and may be termed the ventral protractor. The first runs directly backwards, the second obliquely backwards and upwards ; both are inserted into the cornua at the posterior end.

Of the four pairs of muscles, then, three are protractors, whose function it is to thrust the buccal cavity forwards. As to how far out of the head the chamber is thrust, and what purpose the protraction serves, it is not possible to say. Only a small amount is ever observed in the living insect, or can be brought about in dissections of fresh material. When protraction occurs the teeth at the mouth opening are rotated on their bases so that their points are turned outwards, the rotation, which can often be seen to have occurred in fixed preparations, being a result of their position and method of attachment. It should also be noted that when the chamber is thrust forwards the origin and insertion of the dilator muscle will be approximated, so that the course of the muscle will be vertical.

The membraneous portion of the canal, which connects the buccal cavity and the pharynx, is bent into a short loop in the resting position, passing upwards, backwards, and again downwards, so that in some sections it may be cut across twice. Its wall is thick and tough, but it has no dilator muscles attached to it. The presence of this loop allows for the necessary extension when the buccal cavity is thrust forwards. The loop is situated about the level of the insertion of the antennae.

The pharynx appears in sections as an irregularly tri-radiate structure, composed of one dorsal and two lateral plates of chitin, with a smaller plate ventrally in the anterior part of the wall. The separate plates are united to one another by short bands of membrane, the whole structure closely resembling the corresponding organ in the mosquito. Posteriorly the lumen contracts gradually, and the wall is reduced in thickness, until a very narrow and thin-walled oesophagus is produced.

The pharynx and its musculature

To each of the dorsal and lateral plates of the pharynx there is attached a strong dilator muscle, which passes inwards from the wall of the head. The dorsal muscle is divided into several bundles, and is situated a little anterior to the lateral ones (Plate LXVII, fig. 3). In addition there are well-defined sphincter muscles, which are arranged in two sets, one anterior and the other posterior to the dilator fibres, with which they intermingle to a certain extent. They are attached to the angles of junction of the plates which make up the wall of the pharynx. The posterior division of the sphincter is continued into the wall of the oesophagus, and is gradually reduced in size as it passes backwards, disappearing entirely before the oesophagus enters the substance of the brain. The arrangement of these sphincter muscles makes it possible for the pharynx to be shut off from the buccal cavity in front and from the oesophagus behind.

In addition to the muscles which regulate the size of the pharynx there is another pair which passes to the chamber from the posterior part of the head. These arise from the lateral wall of the head cavity posterior to the brain, and pass inwards and forwards, converging towards the oesophagus, with which they pass between the supra- and infra-oesophageal ganglia, the substance of the muscle being replaced by tendon as it passes forwards. These tendons spread out to gain insertion over a considerable area of the wall of the pharynx, and probably also pass forwards to reach the tube which connects it with the buccal cavity. Their position suggests that they represent the retractors of the oesophagus in *Tabanus* (Plate V, fig. 1), and that their function is to retract the buccal cavity at the end of the act of sucking, by reducing the membraneous portion of the canal to the loop which it forms in the position of rest.

In the region of the looped portion of the canal there are several strong bands of muscle which pass obliquely from the middle line dorsally to the lateral walls of the head, in the region of the antennae, extending as far as the origins of the dilator muscles of the pharynx. These are not attached to the stomodaeum at any point, so that their only action can be to approximate the dorsal and lateral walls of the head, and thereby to reduce its transverse diameter. The most probable function for these muscles would appear to be the increase of the intracranial pressure; an alternation of contraction between these muscles and the dilator muscles of the pharynx and buccal cavity would materially assist in the propulsion of the blood from these chambers into the oesophagus.

The Proboscis and its sheath

The proboscis of the louse is enclosed, in the position of rest, in a membraneous sheath, which, as already stated, extends from the level of the mouth opening to the posterior end of the head, and represents an invagination of the integument. In most sections this sheath appears as very much wider than it normally is, on account of the shrinkage of the soft parts in which it lies. It is for the most part homogenous and structureless, though here and there a few hypodermal cells of the ordinary type can be distinguished in the wall. The constituent parts of the proboscis itself are very difficult to isolate in so small an insect as the body louse, in which, moreover, they are more delicate than in *Haematopinus*. Three stylets can be seen in dissections, corresponding to those already mentioned as seen in sections of the head. The most ventral of these is the labium, which has the shape of a long and narrow gutter, in which the other parts rest. In section (Plate LXXI, fig. 2) it appears as a V-shaped trough. At the posterior end it broadens out considerably, to form a structure which recalls the ' bulb ' in the proboscis of the blood-sucking Muscidae (see page 52). Its distal end is obliquely truncated and ill-defined. Dorsal to it lie the two maxillae, long and narrow blades of very delicate chitin, with numerous fine serrations on their external borders. In sections the two blades appear as concave troughs, open dorsally, and apparently united to one another by their internal borders, forming two parallel channels ; probably in the living louse the two external borders are bent inwards in contact with one another, so as to form a closed tube up which the blood can flow. The inner edges of the blades are certainly softer than the external in cleared preparations, and would therefore undergo more shrinkage during fixation. Below the two maxillae lies the hypopharynx, which is so delicate a structure that it can only be recognized in dissections by the presence of the salivary duct, which runs along its whole length. The duct appears in sections (Plate LXXI, fig. 2) as a circle of delicate tissue, incomplete on the ventral surface ; this gap in the wall is quite possibly due to shrinkage of the soft parts. All the structures at the base of the proboscis are so closely compressed and so firmly bound down to one another by fibrous tissue that it is not possible to determine their relations without a series of much thinner sections than can be prepared by ordinary methods. The lumen of the salivary duct is so small that it cannot be followed beyond the termination of the hypopharynx.

Musculature of the proboscis

It was shown by Schiödte, who cut off the head of a louse while in the act of feeding, that the proboscis is actually thrust out of the head during the act of feeding, as one would expect on anatomical grounds, and as can be readily shown in dissections. It is of some interest, therefore, to look for the muscles by which the acts of protraction and retraction are brought about. Such are to be found in the posterior part of the head, though, for the same reasons which render the relations of the parts of the proboscis itself so obscure in this region, it is by no means easy to determine their precise attachments. The protractor muscles are of relatively large size; they arise from the whole extent of the lateral wall of the posterior part of the head (Plate LXVII, fig. 4), behind the brain, the fibres converging in a fan-like manner as they pass around the large mass of nervous tissue which is passing to the neck, and are inserted into the lateral angles of the two chitinous gutters which represent the proboscis in this region. Their general direction is downwards and backwards, and their contraction must therefore have for its result a forward thrust of the proboscis in its sheath. The retractor muscles which oppose this pair are less easy to define. In all sections about the base of the proboscis a considerable number of bundles of muscular and fibrous tissue are to be seen, which do not extend forwards beyond the base of the proboscis, but can be traced backwards to the neck, where they are inclined outwards to the chitinous walls. Some of these probably represent retractors of the labium, others retractors of the maxillae.

Mechanism of the mouth parts and sucking apparatus

Without insisting too strongly on the functions of muscles the anatomical relations of which have not yet been determined with precision, one may venture to sum up the mechanism of the proboscis and sucking apparatus as follows. The anterior end of the head is thrust against the skin of the host with the teeth in their normal closed position, the hind end of the body being at the same time elevated in order to assist the insect in gaining a purchase, and to bring the mouth parts into a suitable position. The protractor muscles of the buccal cavity then contract, and as the organ is thrust bodily forwards the teeth are rotated on their bases so that their points are turned outwards and thrust into the skin. Possibly this action is repeated several times until the outer cuticle is pierced and the head firmly attached to the skin. According to many observers, among them Pawlowsky, the most recent writer on the subject, the louse chooses the opening of a sweat gland for its point of puncture.* The next occurrence is the protraction of the proboscis from its sheath into the wound. It emerges at the mouth orifice between the two rows of teeth which make up the circlet, and is alternately protracted and retracted until the teeth on the maxillae have bored a hole down to the level of blood. The maxillae then form the channel up which the blood flows to the buccal cavity, and at the same time the saliva is conveyed downwards through the hypopharynx. The dilator muscles of the buccal cavity, which are already brought into a suitable position by the forward displacement of the chamber, then contract, and bring about a negative pressure which draws up the blood from the wound. While this is going on the sphincter between the buccal cavity and the pharynx is closed. As soon as the buccal cavity is full this sphincter relaxes, and the dilator muscles of the pharynx come into action and withdraw the blood from the buccal cavity, the sphincter posterior to the pharynx remaining closed. The blood flows in a straight course to the pharynx, as the bend in the tube which connects it with the buccal cavity is undone when the latter is thrust forwards. When the pharynx is full the sphincter posterior to it relaxes and allows the blood to flow into the oesophagus, probably with the assistance of the muscles which pass from the dorsal to the lateral walls of the head, the contraction of these bringing about an increase in the intra-cranial pressure. When the feed is completed the buccal cavity and the proboscis are replaced in position by means of their retractor muscles.

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* The authors have never been able to satisfy themselves, even after repeated observations, that this is actually the case.

The above account is of course very incomplete. One would like to know, for instance, whether the maxillae alone are protracted during the making of the wound, and to what extent the teeth at the mouth aperture take part; and how the food is transferred from the tube formed, as seems so probable, by the maxillae, to the buccal cavity, with which it is not directly continuous.

In *Haematopinus*, which, according to Enderlein, is a more primitive form than *Pediculus*, there is a pair of two-jointed mandibles in addition to the maxillae. It is noticeable that in those lice which live on thick-skinned animals, such as pigs and buffaloes, the proboscis is much longer than in the human louse, and may extend into the anterior part of the thorax.

About the level of the pharynx there is a pair of glands which open into the sheath of the proboscis, and probably represent salivary glands.

The glands of the proboscis sheath

They are simple and tubular, and are thrown into one or two coils, so that each may be cut several times in sections (Plate LXVII, fig. 3). They lie in the loose tissue on each side of the sheath, and open into its lateral angles. The walls are composed of a simple flattened epithelium set on a rather thick basement membrane. Pawlowsky, who was apparently the first to notice these structures, suggests that they furnish a secretion which acts as an irritant in the wound, or else serves to lubricate the proboscis. Their occurrence in this situation is of some interest, as they might

PLATE LXVII

Figure 1.—Transverse section through the head of [illegible] [illegible], anterior to the insertion of the antennæ and just in front of the opening of the [illegible] canal. The buccal cavity of the [illegible] [illegible], the [illegible] the [illegible] [illegible] the lower the two are connected by a [illegible] edge [illegible] the wall of the [illegible]. The dilator muscle of the buccal cavity, passing [illegible]. The dorsal and median [illegible] passing [illegible] to the [illegible] into the [illegible] part of the buccal cavity, [illegible] and [illegible] protractor muscles, passing [illegible] and the proboscis. [illegible] the body [illegible]. × [illegible].

Figure 2.—From the same series, just anterior to the [illegible] of the antennæ. [illegible] antennæ; [illegible] olfactory [illegible] process from the [illegible] [illegible] × 290.

Figure 3.—A section from the same series, at the level of the [illegible]. [illegible] and [illegible] dorsal dilator muscles of the pharynx, [illegible] of the [illegible]; [illegible] [illegible] the [illegible] trachea; [illegible] ganglion; [illegible] proboscis [illegible] of the [illegible]; [illegible] × 290.

Figure 4.—A section from the same series, behind the brain, at the [illegible] wall of the head. [illegible] [illegible] passing to the [illegible] of the proboscis; [illegible] retractor of the proboscis; [illegible] the labium. The two channels [illegible] of the [illegible] are probably the [illegible] of the [illegible]. × 290.

Figure 5.—[illegible] longitudinal section through the head. The [illegible] from which this was drawn was not quite [illegible], the [illegible] [illegible] the front of the [illegible] protractor muscles of the [illegible]. The salivary gland passing into the [illegible] of the pharynx [illegible] muscles of the pharynx. The pharynx and oesophagus are [illegible] muscles, which reach the [illegible] and the buccal cavity, passing between the [illegible] and the [illegible] oesophagus [illegible] and [illegible]. Some of the [illegible] muscles of the pharynx [illegible] and passing to the [illegible] of the proboscis, mainly [illegible]. There is always a large amount of fat body in the lateral wall of the head. × 290.

PLATE LXVII

Figure 1. Transverse section through the head of *Pediculus vestimenti*, anterior to the insertion of the antennae and posterior to the opening of the proboscis sheath. The central cavity is the buccal cavity, b.c., the ventral one the proboscis sheath, pb.s.; at this level the two are connected by a membraneous expansion from the wall of the sheath. d.b.c., the dilator muscle of the buccal cavity, passing obliquely to its insertion. d.pr., the dorsal and median set of protractor muscles, passing backwards to be inserted into the posterior part of the buccal cavity. l. pr., v.pr., the lateral and ventral protractor muscles, passing to the fulturae. pb., the proboscis. f.b., a fat body cell. × 260.

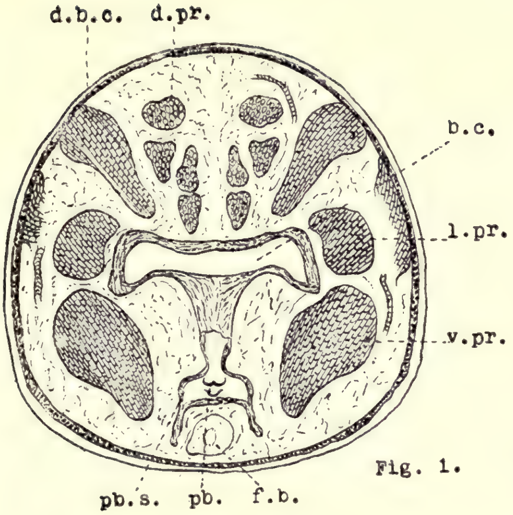
Figure 2. A section from the same series, just anterior to the level of the insertion of the antennae. ant., antenna. ft., the fulturae. br., a median process from the brain. Other letters as above. × 260.

Figure 3. A section from the same series, at the level of the eyes. l.d.ph., lateral, and d.d.ph., dorsal, dilator muscles of the pharynx. sph., sphincter muscle of the pharynx. r.ph., retractor muscles, passing forwards. tr., trachea. gl., cephalic gland (salivary ?). v.pr., ventral protractor muscle of the proboscis. ha., haematocoele. e., eye. × 260.

Figure 4. A section from the same series, behind the brain, at the posterior end of the head. oes., oesophagus. n.c., nerve commissure passing to the neck. l.pr.p., lateral protractor of the proboscis. p.rt.p., retractor of the proboscis. lb., the labium. The two chitinous slips in front of the anterior lamina are probably the basal parts of the maxillae. × 260.

Figure 5. A vertical longitudinal section through the head. The section from which this was drawn was not quite straight, the posterior part being to the right of the middle line. pr.mu., protractor muscles of the buccal cavity. ft., fulturae. gl., gland opening into the sheath of the proboscis. sph., sphincter muscles of the pharynx. The pharynx and oesophagus are not shown. rt.ph., retractor muscles, which reach the pharynx and the buccal cavity after passing between the supra- and the infra-oesophageal ganglia, s.g. and i.g. d.d., fibres of the dilator muscles of the pharynx. n., nerve cord passing to the neck. mu.pr., muscles at the base of the proboscis, mainly retractors. f.b., fat body. There is always a large amount of fat body in the ventral wall of the head. × 210.

PLATE . LXVII.


d.b.c.
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f.b.

Fig. 1.

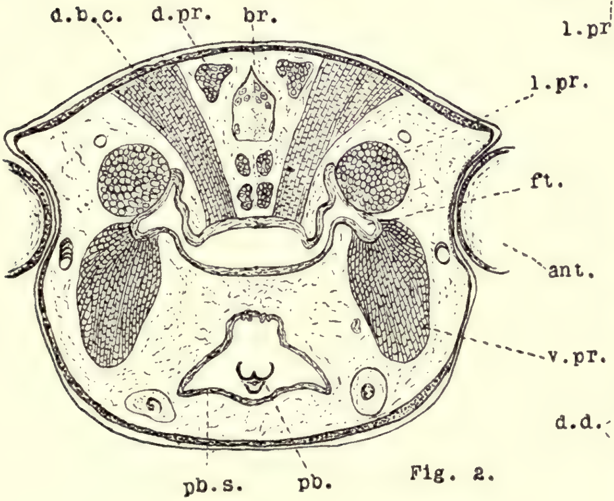
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Fig. 2.

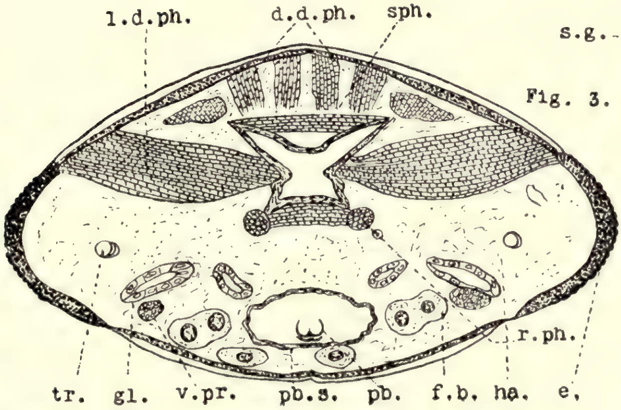
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Fig. 3.

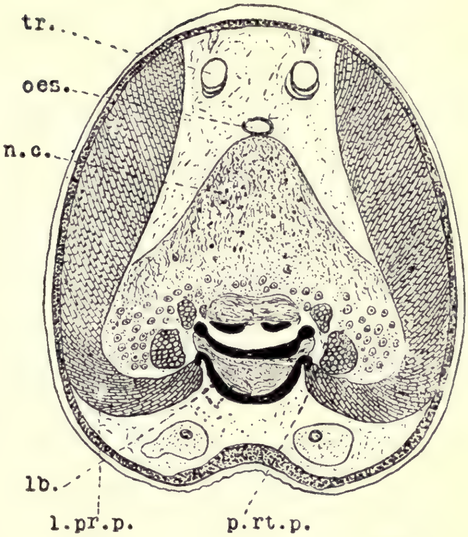
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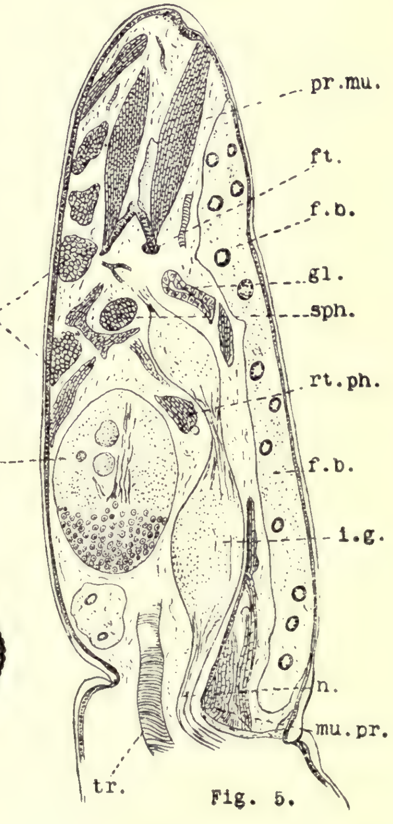
Fig. 4.


pr.mu.
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d.d.
sph.
rt.ph.
s.g.
f.b.
i.g.
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mu.pr.
tr.

Fig. 5.

provide a mode of exit from the body for a parasite. They are extremely small, and cannot be recognized in dissections.

Certain points regarding the nomenclature of the parts should be noted, as the size and shape of the proboscis and sucking apparatus are used as taxonomic characters. The part described in the foregoing as the buccal cavity is termed by Enderlein the *pharynx*; its lateral thickenings are the *fulturae*. The length of the proboscis (*Rüssel*) is also taken into account. The chamber described as the pharynx, and corresponding to the pharynx of the mosquito, is termed by the same author the *larynx*. In the subsequent key and the descriptions of the genera Enderlein's terms will be retained as in the original.

The sucking apparatus and the proboscis can be readily seen through the integument in cleared preparations.

The thorax

The *thorax* is relatively small, and does not show complete segmentation. It is flattened dorso-ventrally, and is much more chitinized at the sides than on the dorsal or ventral surfaces. Usually there are strong bars of chitin passing inwards from the insertions of the legs to act as apodemes for the attachment of muscles. In the middle of the ventral surface there is a single sternal plate, the shape of which forms a useful distinguishing feature (Plate LXVIII, figs. 5, 6 and 7). In nearly all the genera there is a single pair of stigmata on the lateral borders of the mesothorax; in some forms the metathorax also bears stigmata, and rarely there may be a small one on the prothorax.

The legs

The legs are strongly developed, in accordance with the mode of life of the louse, which demands appendages adapted for clinging firmly to the hairs and skin of the host. How well they serve their purpose is demonstrated when one attempts to remove a louse from a rough piece of cloth. Each leg consists of a coxa, trochanter, femur, tibia and tarsal joint. The *coxa*, which articulates with the thorax internal to the lateral border, is broad and oval in shape; the *trochanter* is smaller and narrower; the *femur* has the shape of a short cylinder; the *tibia* is large and stout, and is provided with a thumb-shaped process at the inner side of its distal end, which opposes the terminal claw in much the same way as that in which the thumb of one's hand opposes the index finger. The *tarsal joint* is about the same length as the tibia, or a little shorter, but is much thinner. It terminates in a strong recurved claw, the concave side of which is roughened and thrown into ridges. In *Haematopinus* there is a small triangular plate set with elongate and pointed spines, between the tibia and the tarsus; Enderlein distinguishes this as the *pretarsal sclerite*. (Plate LXVI, fig. 2)

The abdomen

The *abdomen* is flattened in the dorso-ventral direction, and has usually the shape of an elongated ovoid; the contour is more rounded when the ovaries are mature or when the mid-gut is distended with blood. It consists of nine segments, each of which has a tergite and sternite except the first, in which, as in the flea, the sternite is wanting. The tergites and sternites are only thinly chitinized as a rule, while the pleural plates which connect them together may be very strongly developed and heavily pigmented; in *Pediculus* and in many species of *Haematopinus* the pleurae form a conspicuous festooned border on each side of the abdomen, the divisions between the segments appearing as notches. The shape of these pleural plates, and the number and disposition of the hairs or spines with which they are adorned, are used to a large extent in the differentiation of species, especially in the genus *Haematopinus*. The ninth segment is modified for sexual purposes, and differs in the two sexes, serving as a ready means of distinguishing them. In the male, as, for example, in *Pediculus* (Plate LXVI, fig. 6), the tip of the abdomen is produced to a rounded point, at the apex of which the penis projects, while in the female (fig. 5) the two sides are distinctly separated from one another, leaving a notch in the middle line.

The *stigmata* are situated on the pleural thickenings of the abdomen, and appear as clear spaces in preparations. They are usually present on the third to the eighth abdominal segments.

External genitalia

The *external genitalia* of the male are of a comparatively simple type. The penis consists of two pairs of chitinous rods, lying one in front of the other in the terminal segment of the abdomen, and articulated by a moveable joint. The anterior pair are deeply pigmented, and are conspicuous structures in cleared preparations; the posterior pair converge towards one another at the distal end of the abdomen, and often project a little beyond the last segment; they are in close contact with one another, and convey the ejaculatory duct to the exterior between their inner surfaces. The articulation between these two sets of rods, the object of which is to enable the penis to be thrust out and retained in position in the genital opening of the female during copulation, is a complex one, and is acted upon by an intricate arrangement of muscles.

The external genitalia of the female (Plate LXVI, figs. 3 and 4) are the modified sternites of the eighth and ninth segments. The last segment may bear more or less conspicuous eminences, projecting from the end of the body. Anterior to these are two lateral elevations or thickenings in the chitin, the *gonopodia*, which may be small and inconspicuous, or large. The genital aperture lies between these two pairs of structures. The shape and vestiture of these parts provide important taxonomic characters ; usually each is provided with a row of bristles, which may be very conspicuous.

The integument of the louse is of a tough and leathery consistence, and is strengthened by a deposit of chitin at certain points, such as the lateral borders, and in parts of the head. As a rule it is not heavily pigmented, and the mid-gut can be seen through it when the latter contains the usual black residue of blood. The vestiture consists of hairs and bristles of varying length and size, arranged for the most part in transverse rows on the tergites and sternites ; the hairs are usually longer on the posterior segments than on the anterior, and are recumbent and directed backwards.

CLASSIFICATION AND DESCRIPTION OF IMPORTANT FORMS

The following classification of the Anoplura is that adopted by Enderlein, who recognizes four families, including in all fifteen genera.

- Fam. PEDICULIDAE, Leach.
  - Sub-Fam. PEDICULINAE, Enderlein.
    - Genus PEDICULUS, L.
    - „ PHTHIRUS, Leach.
  - Sub-Fam. PEDICININAE, Enderlein.
    - Genus PEDICINUS, Gervais.
- Fam. HAEMATOPINIDAE, Enderlein.
  - Sub-Fam. HAEMATOPININAE, Enderlein.
    - Genus HAEMATOPINUS, Leach.
  - Sub-Fam. LINOGNATHINAE, Enderlein.
    - Genus LINOGNATHUS, Enderlein.
    - „ POLYPLAX, Enderlein.
    - „ HOPLOPLEURA, Enderlein.
    - „ HAEMODIPSUS, Enderlein.
    - „ SOLENOPOTES, Enderlein.
  - Sub-Fam. EUHAEMATOPININAE, Enderlein.
    - Genus HAEMATOPINOIDES, Osborn.
    - „ EUHAEMATOPINUS, Osborn.

Fam. ECHINOPHTHIRIIDAE, Enderlein.
Genus ANTARCTOPHTHIRUS, Enderlein.
ECHINOPHTHIRIUS, Giebel.
LEPIDOPHTHIRUS, Enderlein.
Fam. HAEMATOMYZIDAE, Enderlein.
Genus HAEMATOMYZUS, Piaget.

Enderlein gives the following key for the identification of the above:—

1. Legs formed for clinging. Tibia and tarsus usually very short and thick. Tibia with a thumb-like process. Head without tube-like prolongation anteriorly **3**
   Legs not formed for clinging. Tibia and tarsus very long and slender. Tibia without thumb-like process. Head with a long tube-like prolongation anteriorly, at the point of which the mouth opening is situated . . . . . . **Haematomyzidae 2**

2. Antennae five-jointed . . . . **Haematomyzus.**

3. Body broad and flat. Meso- and metathorax each with a pair of stigmata; stigmata on the second to eighth abdominal segments. Eyes wanting; posterior part of the head broadened out at the sides. Tibia with short, strong, thumb-like process; pretarsal sclerite present. Gonopodia in the female elongated, narrow, produced forwards in the middle. Antennae four-jointed. Thick short spines distributed over the body . . . . **Echinophthiriidae 4**
   Body flattened. Stigmata on each side of the mesothorax only, and on the third to the eighth abdominal segments. Antennae with three or five joints. Tibia with a thumb-like process **6**

4. Antennae four-jointed **5**
   Antennae five-jointed. Thorax and abdomen thickly covered with scales, especially on the dorsal surface. A median stripe on the dorsal surface, broadening out posteriorly, without spines . . . . **Antarctophthirus.**

5. Entirely without scales. Abdomen above and below with about three rows of long and strong bristles, equally distributed . . . . **Echinophthirus.**
   Only the dorsal surface of the thorax and abdomen covered with scales. Median portion of the dorsal surface of the abdomen without spines . . . . **Lepidophthirus.**

6. Eyes large, projecting, and distinctly pigmented. * Pharynx short and broad. Fulturae very strong and very broad, with broad arms. Proboscis short, hardly reaching to the thorax. Antennae with five or three joints . . . . **Pediculidae.**
   Eyes very indistinct or absent. Pharynx long and narrow. Fulturae very narrow and lying close to the pharynx. Proboscis very long. Antennae with five or three joints . . **Haematopinidae 9**

7. Antennae three-jointed † . . . . **Pedicininae**
   Pedicinus.

* *See page 539.* † *See footnote, p. 546.*

Antenna five-jointed . . . . **Pediculinae** 8

8. Forelegs slender, with very long and thin claws. The other legs very strong with short thick claws. Thumb-like process of the tibia short and strong. Abdomen very short and broad. First to fifth abdominal segments strongly compressed, so that the stigmata of the third to fifth segments lie apparently in one segment. Fifth to eighth segments with lateral hook-like processes, the penultimate one long, the last very long. The two-jointed telson on each side without cone-shaped process. Gonopodia of the female triangular . . . . **Phthirus.**

All the legs strong. Thumb-like process of the tibia very long and thin, covered with strong bristles. Forelegs a little more compact and stronger than the rest. Abdomen elongated, moderately narrow, the segments not compressed together; without lateral hook-shaped process. The two-jointed telson bears on the under surface posteriorly a cone-shaped process on each side. Gonopodia of the female clamp-like and bent inwards. . . . . **Pediculus.**

9. Antennae with three joints . . . . **Euhaematopininae** 16

Antennae with five joints 10

10. Forelegs the same size and thickness as the others. Eyes rudimentary, situated at the point of a forwardly directed fork-like lateral process of the posterior part of the head. A triangular sclerite between tarsus and the tibia (pretarsal-sclerite). Mandible well developed and two-jointed . **Haematopininae** 11

Forelegs more slender than the rest. Eyes wanting. Hinder part of the head smooth, without lateral forked process. Mandibles rudimentary. No sclerite between the tibia and tarsus . . . . **Linognathinae** 12

11. Thorax and abdomen broad. Third to eighth abdominal segments with chitinized thickenings of the pleura, irregularly bordered, expanded a little outwards, and so giving to the lateral margin a wavy appearance. On each tergite up to the sixth an indistinct, irregular, and rather sharply defined plate, which is wanting in some species. Each abdominal segment bears a transverse row of minute hairs, usually widely separated from one another . . . . . . **Haematopinus.**

12. Abdomen with strongly chitinized tergite, sternite, and pleurite; tergite and sternite partly secondarily divided. Abdominal border appears serrated on account of extension of the pleura backwards and outwards. Hind leg stronger than the middle leg. Claw of the hind leg short and much compressed, and can be fitted into the tarsus 13

Abdomen without sclerites and plates. Border of abdomen smooth. Hind leg the same size as the middle leg 14

13. Abdomen elongated. Fourth to seventh sternites and second to seventh tergites divided each into two plates lying one behind the other. Each of these plates with a transverse row of long and strong hairs. Pleura without serrated process on the inner side. Stigmata small . . . . . **Polyplax.**

Abdomen more or less elongated. Pleura of the third to the sixth segments each provided dorsally and ventrally with a long, pointed, knife-like process, which may have one or two hook-like teeth in front of the point. Fourth to the seventh tergite and sternite each made up of three short secondary segments, each of which is provided with a transverse row of long, scale-like, broad and flat hairs. Third tergite and sternite consisting of two rings each, of which the anterior is the broadest . . . . . . **Hoplopleura.**

14. Each sternite and tergite of the abdomen with two or three transverse rows of very long and closely set hairs. Stigmata especially large. Middle and hind legs nearly equal in size. Head slender or very slender. Proboscis very long. **Linognathus.**

Each sternite and tergite of the abdomen with one transverse row of hairs **15**

15. Stigmata especially small, not raised above the hind borders as tubercles. Middle and hind legs nearly equal in size. The hairs very long. Abdomen elongated, lateral borders entirely smooth and without spines . . . . . . **Haemodipsus.**

Stigmata moderately large, those of the abdomen raised like tubercles, and standing out above the hind border. Abdomen relatively broad and rounded, lateral borders with one strong spine behind each projecting stigma. Claw of the foreleg very long and pointed . . . . . . **Solenopotes.**

16. Femur and tibia of the hind leg bear rectangular, projecting, stalked, sheath-like appendages . . . . **Euhaematopinus.**

Hind legs normal. Posterior side of the end joint of the antenna deeply hollowed out. Abdomen with strongly chitinized pleura, which broaden out posteriorly and overhang the next segment; on this account the lateral borders of the posterior part of the body appear serrate . . **Haematopinoides.**

FAMILY PEDICULIDAE, ENDERLEIN

Body flattened. Head without tube-like projection anteriorly. Proboscis short, barely reaching to the thorax. Pharynx short and broad. Fulturae very strong and very broad, with broad arms. Eyes large, prominent and distinctly pigmented. Antennae three or five-jointed. Stigmata on each side of the mesothorax only, and on the third to eighth abdominal segments. Legs formed for clinging. Tibia and tarsus generally short and thick. Tibia with thumb-like process. (Dalla Torre).

This family is of special interest, as it contains the lice which are parasitic on man and monkeys. It is divided by Enderlein into two sub-families, Pediculinae, with five-jointed antennae, and Pedicinae, in which they are three-jointed. The Pediculinae contains two genera, *Pediculus* and *Phthirus;* the Pedicinae includes only *Pedicinus.*

GENUS PEDICULUS, L.

All the legs strong. Thumb-like process of the tibia very long and thin, beset with strong bristles. Forelegs somewhat compressed and stronger than the hind. Abdomen elongated, rather narrow, the segments not compressed together; without lateral tooth-like processes.

Three species have been included in this genus, viz., *capitis*, de Geer, *corporis*, de Geer *(vestimenti*, Nitzsch) and *consobrinus*, Piaget. The first two are the head and body lice of man; the third was described from a monkey, *Ateles pentadactylus*, and is, according to Neumann, not distinguishable from *capitis*. The lice infecting man are almost the only ones about which much is known except as regards the external structure; their life history and bionomics will be discussed later.

The type of *P. capitis** is the louse found on the head of the European. When living on such a host the species is of a whitish or greyish colour. Lice from the darker races of mankind, however, are of a much darker tint, the colouration affecting especially the chitinous plates on the lateral borders of the abdomen and the ventral surface of the sternum, with the result that such specimens show much more definite markings than the type. In addition to the variations in colour, lice from the several races of man show other variations, such as in the proportionate length of the legs and claws, and the presence or absence of serrations on the latter, by which, according to Andrew Murray, who devoted much study to the question in connection with the origin of the races of mankind, the species may be divided into races corresponding to the races of the human species. Later workers, notably Piaget and Neumann, are inclined to lay less stress on these minor differences; although they undoubtedly occur, they are inconstant, and the distinctions between the races break down when a large number of specimens is examined.

P. vestimenti (Plate LXIX, fig. 5) is the human body louse, and has received its name from the situation in which it is found. The question—possibly an important one for the parasitologist—as to whether it is a distinct species, or only at most a subspecies, has been discussed by Neumann, who considers that it should be regarded as a subspecies under the name of *P. capitis vestimenti*. The differences between the two are certainly very slight, and it is a very difficult matter to distinguish them except from the locality in which they are found. The body louse is said to be as a rule larger than that from the head, and to have more hairs on the integument, its thorax is broader in proportion to its length, and the

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* The louse from which figure 5, Plate LXVI, was made was taken from a Madrassi.

lateral borders of the abdomen are less festooned. The statement made by Piaget, and repeated after him, that there are seven segments in the abdomen of *capitis* and eight in *vestimenti*, is incorrect, as there are eight segments in each. None of these points is very definite, and variations in the particulars noted above are to be found in lice from either the head or the body; the authors have to confess that in many instances they have found it impossible to decide whether a given specimen should be regarded as *capitis* or *vestimenti*.

GENUS PHTHIRUS, LEACH

Forelegs with very long and thin claws. The remaining legs very strong with short and thick claws. Thumb-like process on the tibia short and stout. Abdomen very short and broad. The first to the fifth segments of the abdomen are very strongly compressed, so that the stigmata of the first to the fifth segments appear to lie in one segment. Fifth to eighth segments with lateral tooth-like processes, the penultimate long, the last very long. (Dalla Torre).

This genus contains the single species *pubis*, L., the pubic louse (Plate LXVI, fig. 1). It is distinguished at once from the other pediculi which occur on man by its characteristic body form. The thorax and abdomen are compressed together to form a heart-shaped mass, broadest in front; the abdominal segments are narrower than the thoracic ones, and diminish in breadth from before backwards. The short squat flattened body and the powerful middle and hind legs have given it its popular name of 'crab' louse. As its specific name implies, it is usually found about the pubic region. It is not so common, or so easy to procure, in Madras as the head and body lice.

GENUS PEDICINUS, GERVAIS

The general characters of this genus are those of the Pediculidae, with the exception that the antennae have three joints instead of five.* Three species are recorded, all from monkeys, as follows. *P. eurygaster*, Gervais, from *Macacus sinicus*; *longiceps*, Piaget, from *Cercopithecus mona*; *piageti*, Stroebelt, from *Macacus erythraeus*. *Pedicinus eurygaster*, from the Madras monkey, *Macacus sinicus*, is shown on Plate LXVIII.

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* This statement is made by Enderlein, and repeated by Dalle Torre. Examination of fresh and cleared preparations, however, shows that the terminal joint, which is much longer than the other two, is 'ringed' in two places, each annulation having a circlet of short and fine hairs. It is, therefore, a matter of opinion as to whether there are three joints or five. The drawing was made from a mature female, and is correct as regards the appearance of the antennae. The shape of the body offers a much more evident distinction between the two genera.

FAMILY HAEMATOPINIDAE, ENDERLEIN

Head broadest behind, but not drawn out into a narrow tube anteriorly. Eyes rudimentary or wanting, and may be placed on a short process of the head, directed obliquely forward. Proboscis very long, and may extend backwards to the anterior part of the thorax. Pharynx long and narrow ; fulturae very narrow, and lying close to the pharynx. Mandibles distinct and two-jointed. Thorax broad, usually with sharply defined sternite ; stigmata on the mesothorax only. Legs formed for clinging, the forelegs usually more slender than the other pairs. Pretarsal sclerite present, and a tarsal process on the inner side of the tarsus, directed distally. Tibia with a thumb-like process. Abdomen flattened, stigmata on the third to eighth abdominal segments ; the tergites and sternites often with small chitinous plates, absent in the male. One row of hairs on each tergite and sternite ; these hairs are wide apart and are usually sparsely distributed.

Enderlein divides this family into three subfamilies, as follows:—In the Haematopininae the antennae are five-jointed; the eyes are rudimentary, and are situated on forwardly-directed lateral processes of the hinder part of the head; the forelegs are of the same size and strength as the other pairs; a pretarsal sclerite is present; the mandibles are well developed and two-jointed. In the Linognathinae the antennae are also five-jointed, but the eyes are wanting, and there is no lateral process of the head; the forelegs are more slender than the rest, and there is no pretarsal sclerite. The Euhaematopininae are distinguished from the other two subfamilies by having only three joints to the antennae.

Neumann, in discussing Enderlein's classification of this group, criticized particularly his treatment of this sub-division. The first six of the genera enumerated in the above key represent the original genus *Haematopinus* of Leach, which Enderlein has raised to family rank and divided into two subfamilies, Haematopininae and Linognathinae; the first of these contains the genus *Haematopinus* of Enderlein, the latter the remaining five genera. Neumann regards this splitting up of the old genus as neither useful nor necessary, though he admits it is possible that it may be justified later by the discovery of new forms. For the present he prefers to regard these new genera as subgenera, retaining the original name *Haematopinus*, Leach. He takes exception to *Polyplax* especially, pointing out that the characters on which it is founded are not sufficiently constant, or peculiar to the group of species included. He unites the genus *Hoplopleura* of Enderlein, which contains only the single species *acanthopus*, Burmeister, with *Polyplax* as a sub-genus.

The genus *Haematopinus, sensu lato*, as thus constituted, and representing the six genera of Enderlein, contains the majority of known species of Anoplura, nearly fifty having been recorded. Many of these are well-known parasites of the domestic animals and of the smaller mammals. Some are of considerable size, and have the integument strongly chitinized, especially along the lateral borders.

Haematopinus suis, L. (Plate LXVIII, fig. 3). Head elongated, longer than broad; on each side in front of the antennae seven hairs, and two pairs of hairs near the proboscis. Basal joint of the antenna shorter than the others, which are equal in length. Six fine hairs, more or less marginal, on the frons. Thorax straight at its junction with the abdomen; mesothoracic stigma with a large white peritreme; a very small prothoracic stigma present; the posterior angles form large conical projections; a single very distinct median plate on the sternum, broader than long and broadest in front, with its anterior angles produced, the posterior angles projecting to a less extent; a very small stigma in each anterior angle. The sternal plate is wanting in young specimens; it may be asymmetrical, one of the anterior angles with its stigma being detached. Abdomen without lateral swellings in the adult; borders festooned on account of the projections which bear the stigmata of the second to seventh segments. On the dorsal surface of each segment a brown transverse band, which occupies the middle third of the length; each median band is often formed by two consecutive bands; externally on each side, between the band and the stigmal plate, a small clear brown, slightly chitinized projection. In the male the last segment is not narrowed at the sides; the ventral genital plate is large, 1 mm. long by ·6 mm. broad, and the genital apparatus, seen through it, passes beyond it in front to a distance of ·7 mm. Under the plate there is a membrane set with spines which serves as a sheath for the apparatus.

This is the type of the genus *Haematopinus*, Leach, and is the largest species of the genus. It is found on the domestic pig and on the wild boar in most parts of the world. In spite of its size it is not suitable for the study of the anatomy, as the extremely tough nature of the integument, which can hardly be cut with a dissecting needle, renders it extremely difficult to dissect.

The lice found on domestic pigs of Asiatic origin, and on the wild boar of Asia, differ slightly from those of Europe, and are regarded by Neumann as a subspecies, under the name *H. suis adventicus*. The

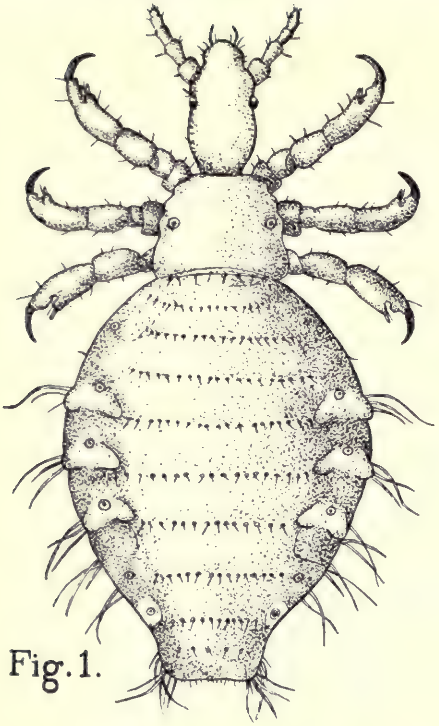

Fig.1.

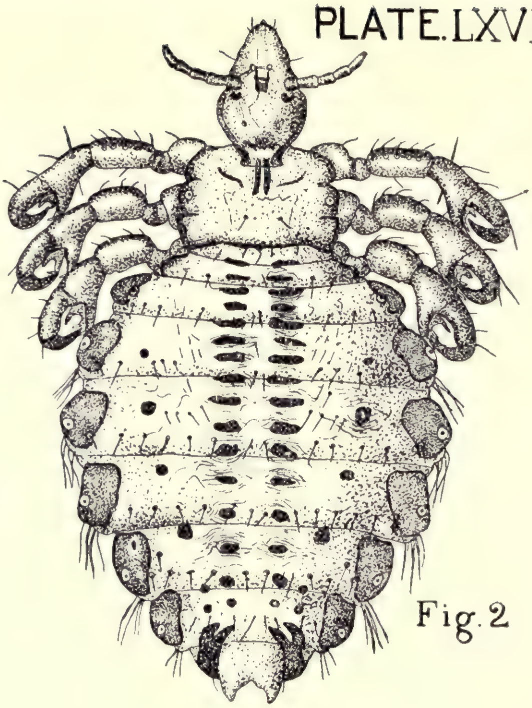

Fig.2

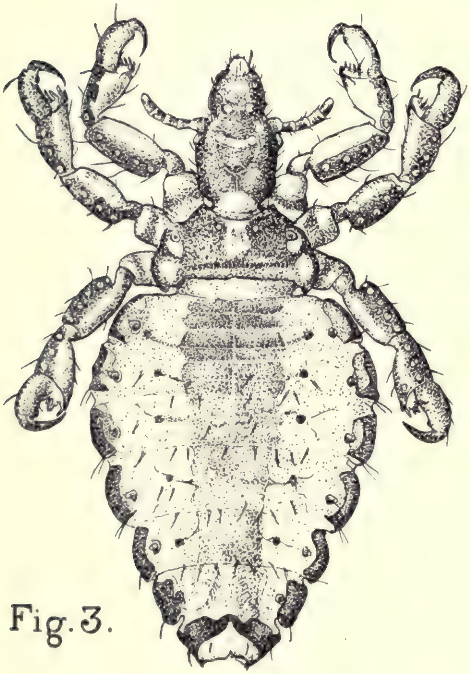

Fig.3.

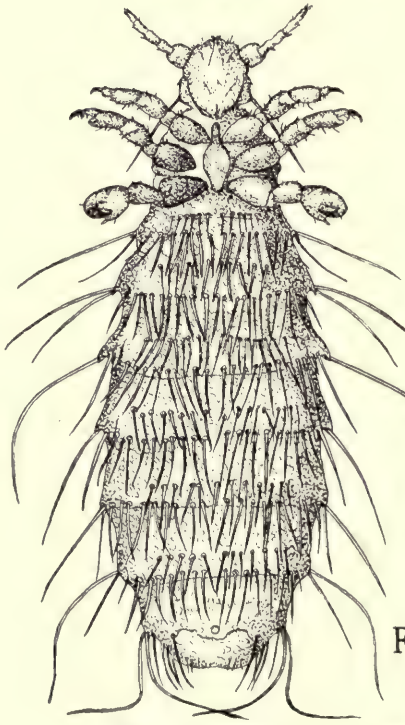

Fig.4.

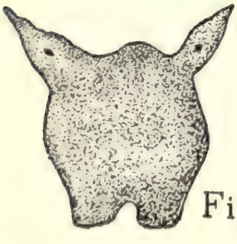

Fig.5.

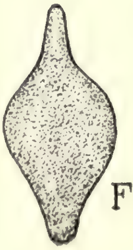

Fig.6.

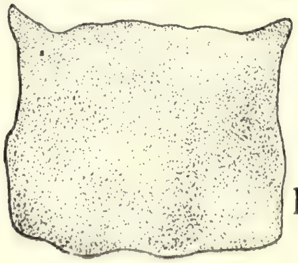

Fig.7.

PLATE LXVIII

Figure 1. *Pedicinus eurygaster*, ♀. × 60.
Figure 2. *Haematopinus tuberculatus*, ♀. × 38.
Figure 3. *Haematopinus suis adventicus*, ♀. × 32.
Figure 4. *H. (Polyplax) stephensi*, ♀. × 80.
Figure 5. Sternal plate of *H. latus*, after Neumann.
Figure 6. The same of *H. (Polyplax) stephensi*.
Figure 7. The same of *H. tuberculatus*, after Neumann.

differences are mainly in the dimensions of the parts. In *adventicus* the body as a whole is more stumpy; the pre-antennal part of the head is longer than in the type species, and the breadth of the thorax is greater than the length of the head, while in *suis* the head is much longer than the thorax is broad; the abdomen is scarcely longer than broad in the female, and as broad as long in the male. The chitinization of the integument is more marked throughout in *adventicus* than in *suis*.

The subspecies *adventicus* is found not only on the domestic pig in Asia and Africa, but also on the English race, a fact which, as Neumann points out in an interesting note on the two forms, is related to the predominence of Chinese blood in the present domestic pig of England.

Several species of *Haematopinus* are found on bovines in various parts of the world. Neumann gives the following key for their identification.

1.	Abdomen with pigmented and projecting pleurae. Anterior legs as strong as the others	2
	Abdomen without pleurae. Anterior legs weaker than the others	4
2.	A bunch of hairs on each side of the abdominal segments	**H. tuberculatus.**
	No bunch on each side of the abdominal segments	3
3.	Abdomen twice as long as broad	**H. bufali.**
	Abdomen scarcely as long as broad	**H. eurysternus.**
4.	Two or three rows of bristles on each tergite and sternite of the abdomen. Head twice as long as broad	**H. (L) vituli.**
	One row of bristles on each tergite and sternite of the abdomen. Head short	**H. (*S*) capillatus.**

H. tuberculatus, Giebel, (Plate LXVIII, fig. 2) is found on the buffalo in India, Tonkin, Sumatra and Roumania. It probably also occurs on the bison, and possibly on the camel. *H. eurysternus* is found on domestic cattle, and may at times be a serious pest. The two species resemble one another very closely, but may be distinguished by the following points. In *tuberculatus* the head is relatively broad; the thorax is broader, the posterior angles more projecting, the sternal plate broader than long and the anterior angles a little projecting; long bristles on the dorsal surface of the abdomen, a bunch of hairs behind each stigmal plate; in the female there is a ventral plate between the gonopodes, in the form of a *fleur de lis*, broadest in the middle, narrowed in front and behind, and preceded by a broad sub-tegmental plate. In *eurysternus* the sternal plate is distinctly longer than broad, has three anterior processes, and is a little constricted in the middle; the plate between the gonopodes is rectangular, and usually longer than broad; there is no subsegmental plate.

H. bufali, de Geer, is found on the cape buffalo. Its head is marked by a deep sinus behind the antennae, which divides it into two parts, of which the anterior is the longer. The terminal joint of the antenna is truncated and darker than the others. The sternal plate is trapezoidal in shape, with its broadest side anterior. Each abdominal segment from the second to the seventh bears a conical process, inclined backwards, at the summit of which is placed the stigma. On the dorsal surface there are two parallel brown bands, extending from the anterior edge of the thorax to the seventh segment of the abdomen; these are separated from one another by a space equal to their breadth; on each side of the abdomen, external to these, there is another narrower band; none of these bands is interrupted at the suture between the segments. The genital plate of the male covers the four last segments on the ventral surface; it is broad in front, narrow behind, with sinuous lateral borders, which are sharply indented in the posterior half; it bears a row of six long hairs parallel to its anterior border.

H. (*Linognathus*) *vituli*, Enderlein, is found on cattle in Europe and in India, and probably in other parts also. In Madras it is sometimes found in very large numbers on calves, often to such an extent as to seriously injure the hide. Animals harbouring such large numbers are usually thin and weakly. The species will be recognized from its habitat and the key to Enderlein's genera, as it is the only species of *Linognathus* which occurs on cattle. The distal end of the abdomen of the female is figured on Plate LXVI, fig. 3.

H. (*Solenopotes*) *capillatus*, Enderlein, was described from cattle at Leipzig. It is the only species of its subgenus. (See key.)

H. (*Polyplax*) *spinulosus*, Burm, is found on *Mus decumanus*, *Mus alexandrinus*, and *Mus sylvaticus*, and is of special interest as being a transmitter of *Trypanosoma lewisi* from rat to rat. Neumann gives the following short description. Pleurae small; those of the second to fifth segments of abdomen approximately triangular, with the base posterior, irregularly and finely dentated, with two short thick unequal bristles, the dorsal angle forming a short spine, the ventral rounded; sixth and seventh oval, with two long hairs. Sternal plate a little longer than broad, pear-shaped, and very slightly coloured.

H. (*Polyplax*) *stephensi*, Christ. and Newst., (Plate LXVIII, fig. 4) is found on the Indian jumping rat, *Gerbillus indicus*, and is probably the transmitter of the interesting haemogregarine with which that animal

PLATE. LXIX.

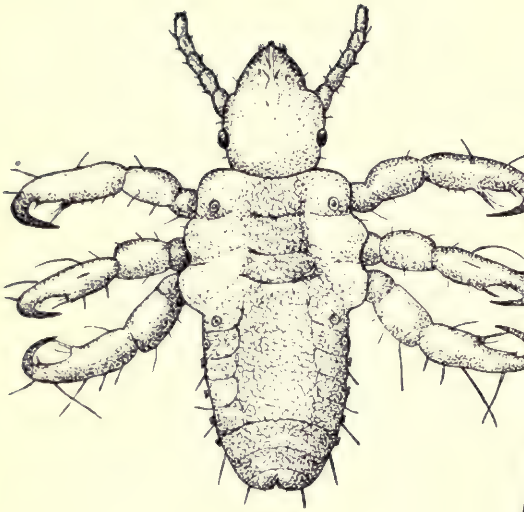

Fig. 1.

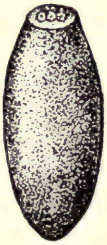

Fig. 2.

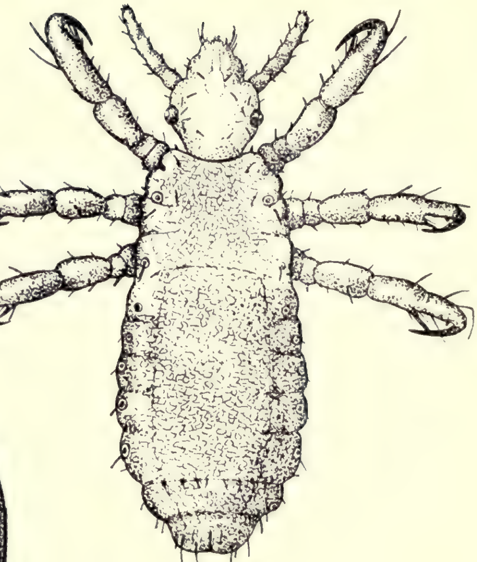

Fig. 3.

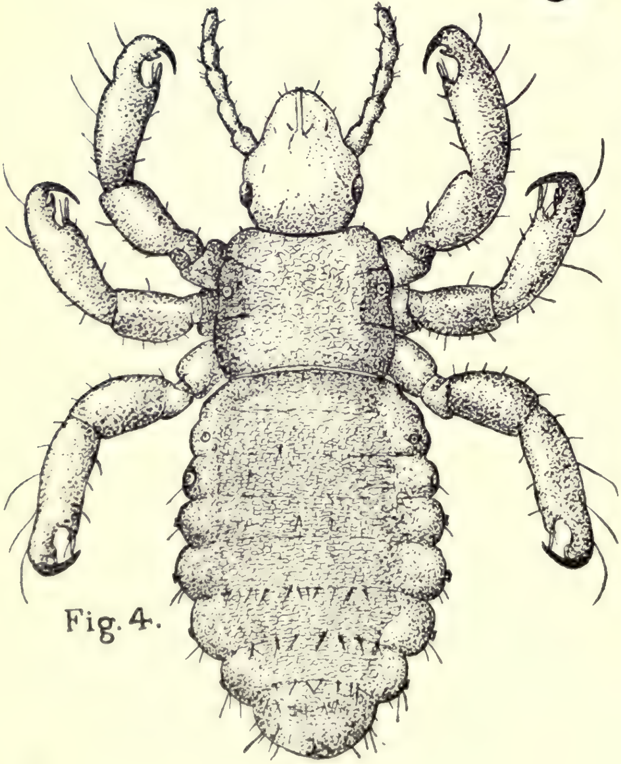

Fig. 4.

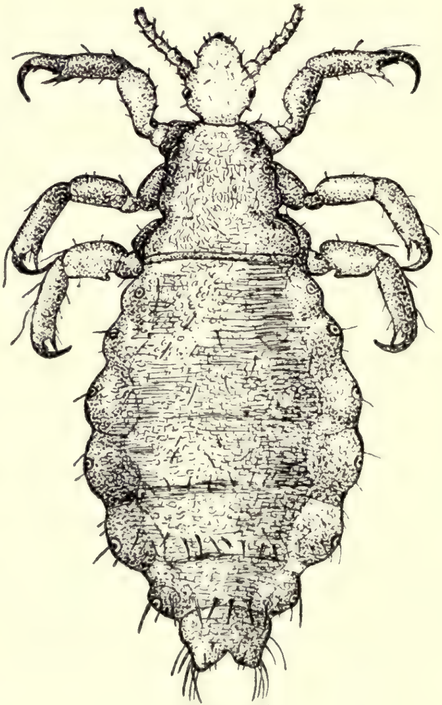

Fig. 5.

PLATE LXIX

Figure 1. *Pediculus vestimenti,* larva. × 58.
Figure 2. *Pediculus vestimenti,* first nymph. × 58.
Figure 3. *Pediculus vestimenti,* the egg. × 30.
Figure 4. *Pediculus vestimenti,* second nymph. × 58.
Figure 5. *Pediculus vestimenti,* ♀. × 20.

is infected. It is a very hairy species, having two rows of long and stout hairs on each of the abdominal segments dorsally, with longer hairs at the sides, which cover up the pleural plates. The head is very short and squat, the antennae being situated almost at its distal end. The pleural plates are oblong, and the dorsal posterior angle of each is produced into a short curved spine. The posterior border of each plate bears two long hairs. The sternal plate is represented in figure 6.

The subfamily Euhaematopininae of Enderlein contains only two species, *Haematopinoides squamosus*, Osborn, and *Euhaematopinus abnormis*, Osborn. Both species are North American, the former from *Geomys bursanus*, the latter from *Scalops argentatus*.

The remaining genera do not contain any species of special interest. *Haematomyzus elephantis*, the elephant louse, is distinguished from all others by having the anterior part of the head drawn out to a tube-like extension.

LIFE HISTORY AND BIONOMICS

Our knowledge of the life history and bionomics of lice rests principally on observations made on the species which infest man, and the following account will accordingly refer particularly to *Pediculus vestimenti*, the body louse. It is of course probable that the other species, of a like habit and similar body structure, will have a similar life history.

Life History of P. vestimenti

The life history of the body louse (Plate LXIX) comprises a period of gradual growth from the larva as it emerges from the egg to the adult or reproductive stage. The period of growth is accompanied by several moults, in which the exoskeleton is cast, but metamorphosis can hardly be said to take place, since the young resemble the adults very closely. The *eggs* (fig. 2) are small oval bodies of a dirty white or slightly yellowish colour, pointed at one end and truncated at the end through which the larva emerges; they are just visible to the naked eye, and are laid on the clothing and hairs of the host, being held in position by means of a sticky substance excreted by the female at the time of oviposition. Only one egg is laid at a time and in each place, though oviposition takes place at frequent intervals. The young larva is able to feed immediately it emerges, although it does not die if kept without food for as long as two days; thereafter it will feed, under artificial conditions, twice a day, and attains its full size in about eleven days, after passing through three moults. The three immature forms are difficult to distinguish from one another except by their size, but they may be distinguished from the adults by the absence of the genital apparatus which characterizes the sexes in the adult stage. In some species of lice the number of prestomal teeth and the number of joints in the antennae is greater in the adults than in the young, and localized chitinizations of the integument, such as the sternal plates, are only developed in the last instar.

According to Warburton, who made a number of exact experiments on the life history of the body louse, a further period of four days elapses before the adults enter upon their sexual functions. The length of life of the adult is given as at least three weeks in the male and a month in the female, under artificial conditions, which, however, approached as closely as possible to the normal. The first egg is laid soon after copulation, and thereafter the female continues to oviposit at intervals during the rest of her life, the large number of eggs laid serving to compensate for the great susceptibility of the species to adverse conditions. Warburton found in one experiment that 124 eggs were laid in twenty-five days.

The time occupied in the growth from egg to adult is apparently dependent on the supply of food rather than on the air temperature. Warburton gives the following details of his experiment, carried out in England in December. The larvae were fed at least twice in each twenty-four hours.

Incubation period	eight days to five weeks.
From larva to imago	eleven days.
Non-functional mature condition	four days.
Adult life	male, three weeks. female, four weeks.

In an experiment carried out by the authors, in Madras in March, with an average daily maximum temperature of 86° F., the following results were obtained. The lice were fed only once in the twenty-four hours.

Larvae hatched on March 11th and 12th, fed on	13th
All moulted on	17th
Second moult on	23rd
Reached adult stage, final moult	29th

Habits

The louse appears to spend most of its life clinging to the hairs or clothing of the host. Their powerful claws and stout muscular legs enable them to take a very firm hold, and they are remarkably difficult to detach. They can, however, move very actively on occasion ; some of the species of *Haematopinus*

(*Polyplax*) from rodents travel so rapidly among the hairs of the host that it is often extremely difficult to catch them with forceps. The antennae are moved from side to side in a very characteristic manner during progression. As shown in the above tables, they will feed twice a day, though one feed is enough to support them in the climate of Madras. When fed artificially in this manner they always take a full meal, the ingestion of blood being accompanied, as in so many blood-sucking insects, by the evacuation of the contents of the hind gut ; the material first passed out consists of small black particles, followed later by apparently unaltered blood.* Adult *vestimenti* usually remain clinging to the cloth on which they are kept throughout the meal, and show no disposition to move away, but the larvae tend to wander actively about, in order, as Warburton remarks, to establish themselves in new positions.

The method of feeding can be easily observed through a lens without disturbing the insect, though the parts are so small and so well concealed that the details cannot be made out. The louse depresses the head till it is in contact with the skin, and elevates the hind end of the body. In a few seconds the pharynx appears as a bright red pulsating spot, showing through the transparent integument of the head ; when a full meal has been taken the abdomen becomes visibly distended, so much so that young and transparent larvae look like small pink spots. The irritation produced by the bite is very considerable in persons who are not habitually subjected to it.

Copulation can often be observed in *vestimenti* in captivity. It occurs, according to Warburton, four or five days after the lice have reached the adult stage. The method by which it is carried out is peculiar, and resembles the habit of fleas. The female louse remains clinging to her hold in the ordinary position, while the male, who is the smaller of the pair, crawls underneath her, his back in contact with the ventral surface of the female, and clasps her second pair of legs with his first pair. The end of the abdomen is then tilted up and the penis inserted. The two remain in this position for a considerable time. Copulation takes place several times in the life of the female, as one might expect from the fact that there is no receptacle for the sperms such as is found in the Diptera and fleas.

The outstanding fact in the bionomics of the body louse—and this applies also to lice from the monkey, pig, and buffalo—is that it is extraordinarily susceptible to even slight changes in its environment, and

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* Nicolle, Blaizot and Conseil state that spirochaetes are never passed out in the faeces of infected lice.

Bionomics

does not thrive apart from its host. Warburton found that the lice on verminous clothing were usually dead when they reached his laboratory, and that they could not be kept alive even when placed in an incubator at a steady body temperature. In a few cases he found specimens able to survive as much as four days starvation, but this was very exceptional. The authors have had similar experiences in the cold weather in Madras, having found that lice taken from the human subject in the early morning and placed on pieces of cloth, in carefully cleaned and dried tubes, were generally dead in the afternoon. In carrying out the breeding experiment detailed above, however, no such difficulty was met with, and the lice were bred from the egg to maturity without any special precautions being taken, and were kept, from the time they hatched from the egg, in tubes on the laboratory table. It has not been ascertained whether it is the comparatively small increase in the temperature, which would not amount to more than ten or fifteen degrees, which makes the difference, or whether it is that the immature stages of lice are more hardy than the adults. Warburton found that newly hatched lice die in 36 hours if not fed; the present writers have found them alive up to two days, a longer period than the adults will usually survive.

The eggs of lice, on the other hand, appear to be able to resist unfavourable conditions to a much greater extent. According to Warburton they may take as long as a month to hatch, a most important fact in considering the possibility of spread by infected clothing, etc.

Breeding Technique

The rearing of lice in captivity is a difficult and troublesome task, as will be readily understood from what has been said with reference to their susceptibility to unfavourable conditions. The difficulty appears to be greater in a cold climate than in hot one. Warburton, who carried out his experiments at a time when the room temperature on some occasions fell considerably below freezing point, succeeded in keeping them alive for over a month and rearing them from the egg by the following method. A female was placed in a glass tube about 3 ins. by ·5 in., together with a piece of cloth on which to rest, and with a male. The tube was then plugged with cotton wool and enclosed in a metal case open at one end, to guard against accidents, and carried close to the person night and day, the lice being fed twice a day. The eggs when laid were allowed to remain on the cloth, as it was found that no matter how carefully they are handled they die if any attempt is made to remove them. The adults are easy to feed, as they remain clinging to the cloth, but the larvae give trouble on account of their tendency to wander about, and only a small number can be handled at one time.

No such elaborate precautions have been found necessary in the warm climate of Madras in the cooler months of the year. In the hot weather, however, it is necessary to keep the lice in a cool incubator with a temperature of about 75° C., and to feed at least twice each day.

Great care should be taken in handling the lice, and they should not be touched with forceps if it can be avoided, as they are very easily injured. When it is necessary to feed them the piece of cloth on which they rest should be taken out of the tube with forceps and applied to the skin; any which pass on to the skin and remain there after they have fed can be picked up with a soft brush. Eggs laid on the cloth may be allowed to remain till they hatch, which may be as long as a month, or the piece of cloth to which they are attached may be cut out and placed in a separate tube. Dark and thick cloth, such as flannel or serge, is the best kind to use.

Method of Carrying out Experiments

In performing experiments with the head louse the following method has been adopted. The head is first thoroughly cleansed, and the hair cut short if necessary. All lice are removed with a fine comb, and any hairs to which nits are attached cut off with scissors. Fresh adult lice, either bred from the egg or obtained from a non-infected individual, are then placed on the head, and the hair covered up with a closely fitting cap of fine muslin. When the lice are required for examination they are removed by means of a fine comb. Body lice may be kept in tubes and fed on the wrist or forearm, as already described.

When experimenting with the smaller mammals, and especially in the case of rodents, it must be borne in mind that the animal may harbour more than one species, and that they may frequent different parts of the body. The Indian squirrel, for instance, harbours one species about the neck and another in the region of the tail.

Before commencing any experiment the animal should be completely freed from lice. This is best accomplished by chloroforming it, and removing the stupified lice with a fine comb, cutting off all hairs to which nits are attached. To ensure that none have been missed the animal should be put back in a cage for a time to allow any remaining ova to hatch, and again examined. A definite number of bred individuals is then placed upon the host under whatever conditions may be necessary.

Experiments with the larger mammals, such as cattle and pigs, are difficult to carry out, as the lice die if kept apart from the host. The plan which offers the best chance of success is to first free the host from its parasites, and then to place a definite number of known history on the ears, which are then enclosed in bags of muslin. If necessary precautions can be taken to prevent the host from scratching off the bag.

INTERNAL ANATOMY

The Alimentary Canal, Plate LXX

The *alimentary canal* of the louse is a simple one, and resembles generally that of *Cimex,* from which it is distinguished, however, by the high position of the Malpighian tubes, the presence of vestiges of rectal papillae, and the absence of a rectal ampulla. When dissected out it is about twice the length of the body of the insect.

The *oesophagus* commences at the posterior end of the pharynx in the head, and passes through the brain in the ordinary manner, lying dorsal to the large nerve cord in the neck. It enters the thorax between the salivary ducts, and joins the mid-gut between its two lateral lobes. The wall is composed of a rather thick and crinkled chitinous intima, usually thrown into many irregular folds, and having only a scanty layer of hypodermal cells. The oesophagus will stand a good deal of stretching without rupture.

The Mid-gut

The *mid-gut* is a large cylindrical chamber, commencing in the thorax and occupying almost the whole of the abdominal cavity. As it receives the blood directly from the oesophagus in the act of feeding, it is capable of considerable distension, and may become so large after a full meal as to produce a visible swelling of the body of the insect, the red blood showing through the transparent integument. During the time digestion is going on its shape is constantly changing on account of the peristaltic contractions of the muscles of its wall, so that it sometimes appears to be constricted in the middle or at the ends, or to have narrower parts. None of these breaks in the contour of the organ is permanent, and in the resting condition the shape conforms generally to that of the cavity in which it lies. When not filled up with fresh blood the chamber contains a variable amount of brownish black granules, the remains of digested blood.

At the anterior end (Plate LXX, fig. 1) the mid-gut is divided into two lobes, one on each side of the oesophagus. These project into the cavity of the thorax, and as they contain the same black granules as are found in the rest of the gut their position is easily recognized in the living insect. They resemble the posterior portions of the organ in structure,

PLATE LXX

Figure 1. The anterior end of the mid-gut of *Pediculus vestimenti* with the salivary glands *in sitû*. oes., oesophagus. sl.d'., the duct of the reniform salivary gland. sl.d''., the duct of the tubular gland. sl.g'., the reniform salivary gland. sl.g''., the tubular glands. The two anterior lobes of the mid-gut are shown. s.c., the specialised cells lying around the oesophagus and the ducts of the salivary glands. × 125.

Figure 2. The specialised cells near the oesophagus, oes. Note the marked distinction between these cells and those of the fat body among which they lie. Compare with figure 4 on Plate LXXI, which is drawn to the same scale. × 550.

Figure 3. Cells of the mid-gut, seen in a transverse section. Note the unusual condition of the nucleus, n., the collection of vacuoles near the lumen, v., and the well defined striated border. c.mu., l.mu., circular and longitudinal muscle fibres. tr., trachea. × 900.

Figure 4. A transverse section through the hind-gut, showing the chitinous intima thrown into folds and furrows which interlock with one another. × 270.

Figure 5. A transverse section through the thorax of *Pediculus*, passing through the anterior lobes of the mid-gut, mg.d. ap., the apodeme formed by the union of the two processes from the posterior part of the head. ha., haematocoele. th.g., thoracic ganglion. mu., muscles of the body wall. l.mu., longitudinal muscles. Other letters as before. × 133.

Figure 6. The alimentary canal of *Pediculus vestimenti*. c., the little mass of specialised cells on the ventral wall of the gut. h.g., hind-gut. ch.p., the chitinous plaques which represent the rectal papillae. Other letters as before. × 45.

PLATE LXX.

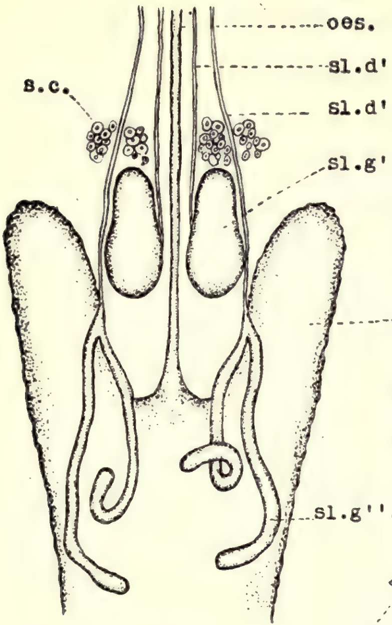
oes.
sl.d'.
s.c.
sl.d''
sl.g'.
mg.
sl.g''.

Fig. 1.

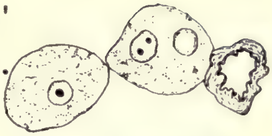

Fig. 2.

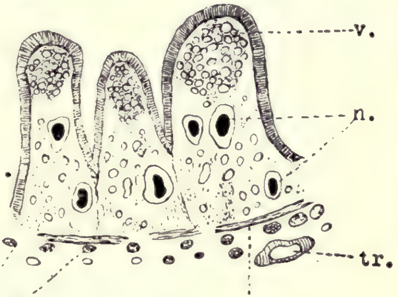
v.
n.
tr.
l.mu.
c.mu.

Fig. 3.

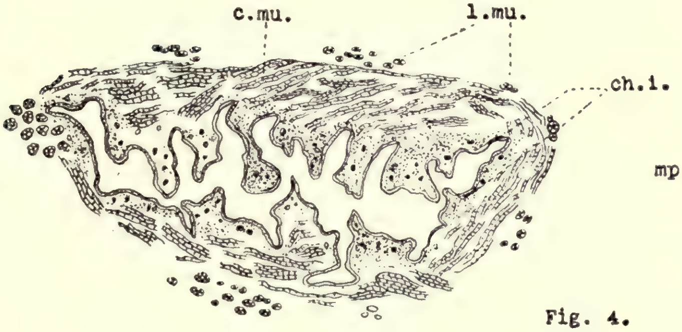

Fig. 4.

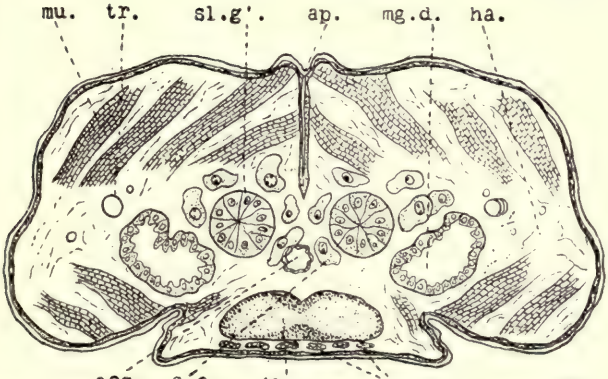
mu.
tr.
sl.g'.
ap.
mg.d.
ha.
oes.
s.c.
th.g.
l.mu.

Fig. 5.

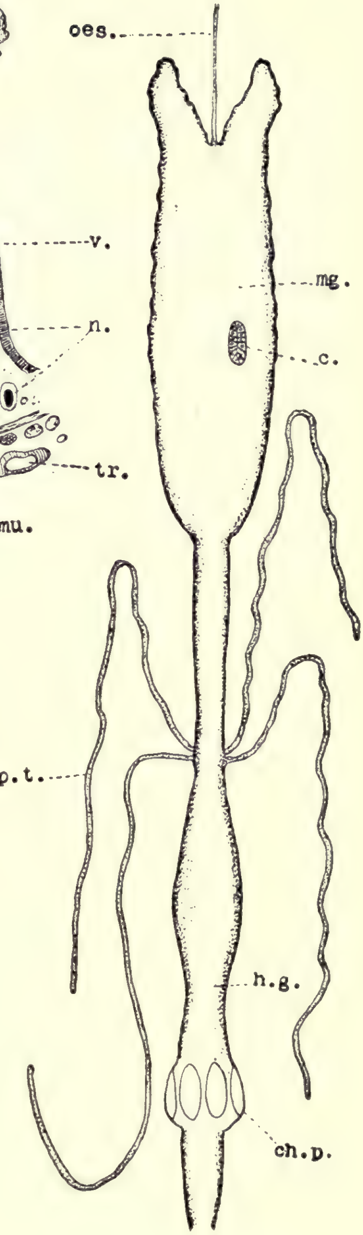
oes.
mg.
c.
mp.t.
h.g.
ch.p.

Fig. 6.

and like it are constantly changing their shape with the contractions of the muscle fibres in the wall.

The wall of the mid-gut (fig. 3) consists of a layer of digestive cells and circular and longitudinal muscle fibres. The cells are cylindrical and somewhat irregular in shape, no two cells being exactly alike, so that the lumen presents an irregular outline in sections. The inner half of each cell is rounded and free from its fellows on each side, and may be slightly swollen. There is a well marked striated border extending all round the free portion of the cell, and a slightly denser and more deeply staining layer immediately internal to this. The projecting portion of each cell contains a collection of small vacuoles set closely together, which probably represent the digestive secretion of the cell collected at this point previous to discharge into the lumen of the gut. Each cell contains from one to three nuclei, differing markedly from those of any of the digestive epithelia so far considered. They are small, irregularly oval in shape, and in sections stained with haematoxylin show a clear area surrounding a central mass of deeply stained chromatin. The remaining portion of the cell contains many large and small clear vacuoles, scattered irregularly throughout the protoplasm. The whole epithelium differs markedly from that of the Diptera or the fleas.

Both the circular and longitudinal muscle bundles are well developed and are regularly arranged. The inner (circular) fibres are closely pressed against the bases of the digestive cells; no basement membrane can be distinguished.

On the right side of the ventral surface of the mid-gut there is a small collection of specialised cells, forming an oval patch, distinctly raised above the level of the rest of the wall, and sharply distinguished in the fresh condition on account of the yellow pigment which the cells contain. Each cell is cylindrical in shape, and is directed inwards towards the lumen, the bases being arranged in the rows of about eleven cells each. The function of these peculiar cells is not known.

The *hind-gut* commences at the point of insertion of the four Malpighian tubes, and at once turns forwards ventral to the mid-gut; after a short course it again turns backwards to reach the anal aperture. It is much narrower than the mid-gut, and is of fairly uniform diameter throughout, though somewhat swollen about the middle of its length. There is no rectal ampulla, the rectum being only distinguished by the presence of certain chitinous plates, probably representing rectal papillae, in the wall.

The portion of the hind-gut anterior to the rectal plates, roughly about two-thirds of the whole, has a wall of a special structure (Plate LXX, fig. 4), apparently designed to prevent the escape of the contents of the mid-gut during digestion. The lining is composed of a thick chitinous intima, produced inwards into conspicuous and irregular processes, which interlock with one another across the lumen so as to entirely close it. A few very small cells can be distinguished outside the chitinous portion, and external to these there is a very strongly developed coat of circular muscle fibres, rather loosely arranged. Here and there a few bundles of longitudinal muscles can be distinguished.

The *rectal plates* (Plate LXX, fig. 6, and Plate LXXI, fig. 5) mentioned above are six in number. Each is oval in shape, the set being arranged with their long axes in the long axis of the gut. They project a little from the external surface, and are conspicuous in fresh preparations. On section they appear as a ring of tissue, apparently mainly chitinous, but with some cells embedded in the centre, completely surrounding the lumen, and separated into six equal portions, concave on the internal surface, convex externally. A very thin band of circular muscle fibres surrounds the whole, while in the angles between the separate plates there are a few small bands of longitudinal fibres. Most probably they represent degenerated rectal papillae; no tracheae can be found entering them.

The *Malpighian tubes* are four in number, and resemble those of the Nematocerous Diptera. Each arises independently from the alimentary tract at the junction between the mid-gut and the hind-gut.

The Salivary Glands

The *salivary glands* (Plate LXX, figs. 1 and 5) lie in the thorax, in association with the oesophagus and the lateral lobes of the mid-gut. There are at least two pairs, one tubular, the other kidney-shaped. The *tubular glands* are closely bound down to the mid-gut, and remain attached to it in dissections. Each consists of two limbs, of about equal length, leading to a common duct. The outer limb is only slightly curved, the inner one bent acutely upon itself. The duct passes upwards to the neck on the outer side of the oesophagus and the kidney-shaped gland. The *kidney-shaped glands* are set side by side external to the oesophagus and between the anterior ends of the lateral lobes of the mid-gut. They are oval in shape, slightly narrowed in the middle, and considerably longer in the antero-posterior diameter than in the transverse. The opening of the duct is situated in a hollow on the inner side, corresponding to the hilum of the kidney, and from this point the

PLATE.LXXI.

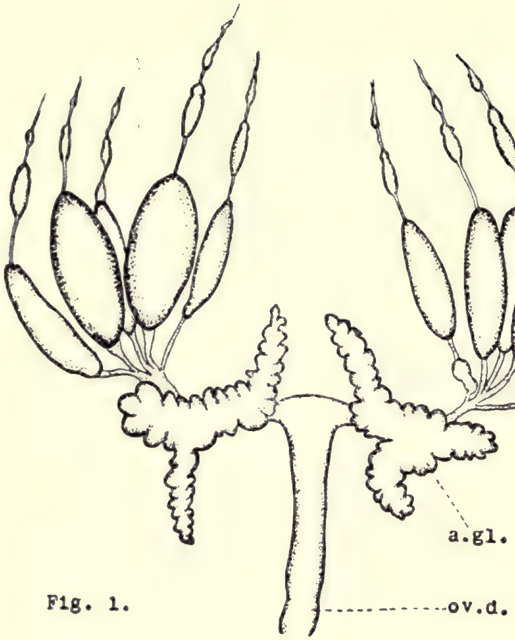

Fig. 1.

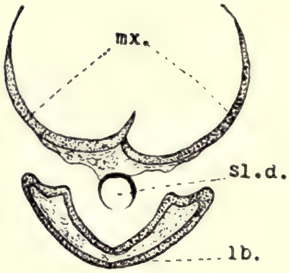

Fig. 2.

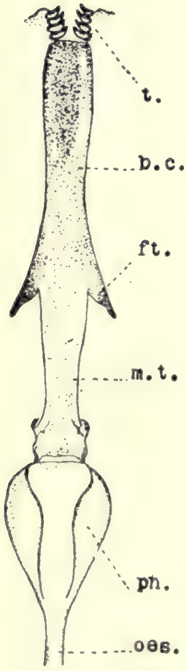
t.
b.c.
ft.
m.t.
ph.
oes.

Fig. 3.

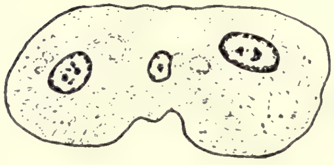

Fig. 4.

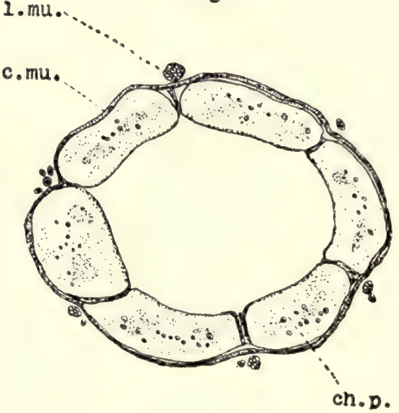

Fig. 5.

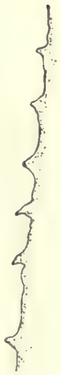

Fig. 6.

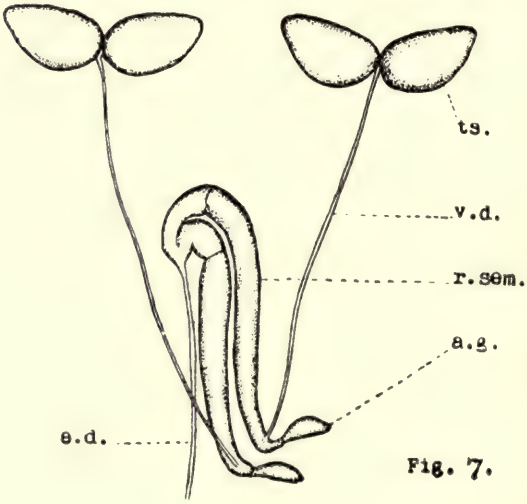
ts.
v.d.
r.sem.
a.g.
e.d.

Fig. 7.

PLATE LXXI

Figure 1. The female reproductive organs of *Pediculus vestimenti* showing the five ovarian tubes, uniting on each side to form an oviduct, which is enveloped in the accessory gland, a.gl. ov.d., the common oviduct. × 33.

Figure 2. The proboscis of *Pediculus vestimenti*, very highly magnified, as it appears in transverse sections through the head. mx., the maxillae. sl.d., the salivary duct. The softer tissue ventral to the maxillae is perhaps the hypopharynx. lb., the labium.

Figure 3. The chitinous framework of the sucking apparatus of *Pediculus vestimenti*, as seen in a cleared preparation. t., the prestomal teeth. b.c., the buccal cavity (the pharynx of Enderlein). ft., the fulturae, or lateral thickenings of the buccal cavity. m.t., the membraneous portion between the buccal cavity and the pharynx. ph., the pharynx (the larynx of Enderlein). oes., the oesophagus.

Figure 4. A cell of the fat body, from the side of the oesophagus. Compare with figure 2 on Plate LXX. × 550.

Figure 5. A transverse section through the hind-gut of *Pediculus*, at the region of the chitinous plates, ch.p. l.mu., c.mu., longitudinal and circular muscle fibres. × 300.

Figure 6. A portion of the edge of the maxilla of *Pediculus vestimenti*.

Figure 7. The male generative organs of *Pediculus vestimenti*. ts., testis. v.d., vas deferens. r.sem., seminal vesicle. a.g., accessory gland. e.d., ejaculatory duct. × 40.

duct turns upwards to the neck immediately external to the oesophagus, and internal to the duct of the tubular gland.

In the region of the salivary glands there is a large amount of fat body, arranged in long and irregular lobules of an opaque white colour. These are closely adherent to the salivary glands and the ducts, and render dissection of this region a somewhat difficult matter. Embedded among the fat body, immediately anterior to the kidney-shaped glands, there is on each side a small collection of round cells (Plate LXX, fig. 2), readily distinguished from the fat body by their more glistening appearance. These are constant in position, and are always found, in sections and dissections, surrounding the oesophagus, though not attached to it in any way. They have no capsule, but appear to be connected with one another by short and pointed processes. The protoplasm of these cells is vacuolated, and contains many fine granules. One, or sometimes two, nuclei are present, and appear as clear vesicles containing a darkly staining central mass of chromatin. No duct has been distinguished with certainty, though in some dissections a fine filament which may perhaps be a duct has been noted passing upwards with the salivary ducts.

Reproductive System. The Male Organs, Plate LXXI

The *reproductive organs* of the louse present some interesting peculiarities. The male organs are quite unlike those of other insects. There is a pair of *testes* on each side; each is a small oval body, and the two of each pair are closely apposed to one another by their broad ends. The *vas deferens* of each side arises at the point of junction of the pair, and passes directly to the posterior end of the abdomen as an extremely fine tube, much finer than could be represented in the drawing (Plate LXXI, fig. 7). The *receptacula seminis* are also paired, each receiving the vas of its own side; they are long tubular structures, slightly narrower at the posterior than at the anterior end, and lie parallel to one another in the middle ventral region of the abdomen, reaching almost as far forwards as the testes. The vas of each side enters its receptaculum at the narrow posterior end, and here there is on each side a small conical accessory gland, attached to and apparently continuous with the receptaculum; in fresh preparations the gland and the receptaculum have the same appearance, and it is only in stained preparations that one recognizes the difference in structure. At the anterior (or distal) end each receptaculum becomes continuous with an efferent duct, without any diminution in the calibre at first; after a very short course these ducts turn backwards in a ventral direction, and at once become narrower and unite with one another. From their point of junction the common channel is continued backwards to the penis as a fine efferent duct. In fresh dissections the receptacula are very conspicuous on account of their translucent appearance and their slight greenish tinge; the testes lie in the anterior segments of the abdomen, and are embedded in fat body, from which they are not easy to remove.

The Female Organs

The female organs of reproduction consist of ovaries, oviducts, a pair of accessory glands, and a common oviduct. Each *ovary* consists of five ovarian tubes, usually divided into three follicles, which are distinctly separated from one another by an interval in which the tube is much constricted. In the mature ovary (Plate LXXI, fig. 1) at least one of the lowest follicles on each side contains a mature or nearly mature egg, while the other follicles of the same rank contain ova at various stages of development, some being only a quarter or a third the size of the largest. The follicles of the second row are always small, and those of the third little more than mere swellings on the tube; it is to be noted, however, that even in these small chambers there is a considerable variation in size. The tube is continued forwards from the smallest follicles as a delicate apical filament, all the filaments converging together in the usual manner. At the lower end of the lowest follicle of each tube the separate tubes, after a short independent course, are collected together and unite to form a duct common to the ovary of the side. The *accessory glands* are situated on and partly conceal this portion of the duct; each is a large and irregularly triradiate structure, resembling more than anything else the three-legged symbol of the Isle of Man; one limb is directed forwards, one backwards, and the other outwards, the whole being closely adherent to the duct. The commencement of the common oviduct lies between them, and from this point the duct passes straight backwards to the genital opening; it is of rather large size, and has much muscular tissue in its wall.

The long duration of copulation in the louse, and the frequent repetition of the act, are of special interest in view of the absence of a receptacle for the sperms in the female, and the relatively large size of the receptaculum in the male. It will be noticed that the conditions found in the ovaries, in regard to the maturity of the eggs in the lowest row of follicles, are in accordance with the observed habits of oviposition. A departure from the type of reproduction usual in insects is frequently to be observed in association with the parasitic habit; the bed bug is a striking case in point.

DISSECTION

The internal organs of lice cannot be dissected out by the methods which succeed in the case of the Diptera, owing to the tough nature of the integument and to the close union between the segments of the exoskeleton. The integument cannot be torn, and there are no weak places between the segments at which it can be easily incised. It is therefore necessary to adopt other procedure.

Exposure of Internal Organs

The following method has been found successful. Cut off the legs as near their junction with the thorax as possible, using a pair of fine scissors, or remove them by cutting through the joint between the coxa and femur with a sharp needle. Remove them from the slide, and lay the louse on its dorsal surface with the head away from the observer, and steady the anterior end with a needle held flat on the thorax or between the thorax and the head. Then take a sharp lancet-like needle and cut off, with one incision if possible, the whole of the lateral margin internal to the stigmata, from the anterior to the posterior end. When this has been done some of the organs, probably the ovaries if they are mature, will slip out through the gap. Then turn the insect round the other way and repeat the manoeuvre on the other side, so that the dorsal and ventral surfaces of the integument are separated from one another except at the anterior and posterior ends. Next thrust a needle under the ventral part of the skin from side to side and, using it as a director, cut transversely across the ventral flap about its middle; the transverse cut is made most easily if the louse is turned over on its ventral surface after the director has been inserted. The two flaps can then be easily dissected forwards and backwards by severing the tracheae attached to them, and in the case of the larger lice they can be cut off with scissors and removed. The internal organs are now exposed.

Removal of the Reproductive Organs

The genital organs lie ventral to the gut, and should be removed first. In the case of the male the long cylindrical receptacula will be recognized at once by their characteristic shape and contour. Pull these forwards and stretch them a little, and the ejaculatory duct, passing to the penis, will be seen. This should be cut across with a needle, and the whole system removed. The testes are placed far forwards in the abdomen and are surrounded by a mass of fat body; if they are not required for examination the vasa can be cut across and the testes allowed to remain *in situ*. In the female the ovaries lie on either side of the gut, but their attachments are very loose, and the separate tubes spread out at once when the cavity is opened. The apical filament should be kept intact as long as possible, to keep them together, and the oviduct sought for and cut across, so that the whole ovary can be removed intact. If the ova are mature they are very easily detached from their follicles, and can be removed with a pipette.

Dissection of the Alimentary Tract

The alimentary tract, from the oesophagus downwards, is removed by freeing it at its two ends and dissecting off the tracheae as they appear. The oesophagus should be cut through by severing the neck, and allowed to retract through the thorax, which it usually does readily enough; if any difficulty arises a little traction will bring it into view. The anterior lobes of the mid-gut should then be reflected to one side, and the whole tract dissected out from before backwards to the anus.

The gut cannot be dissected out through the last segments, as in the case of the Diptera, because the integument is far too tough to be torn even if it is incised at the sides. The lateral margins internal to the pleural thickening are the only places where the skin can be cut without injuring the internal structures.

The Salivary Glands

The salivary glands are the most difficult of all the organs to isolate. They lie in the thorax, and are closely surrounded by the large muscles of the legs, and are moreover deeply embedded in a mass of fat body. The tubular glands are bound down to the anterior end of the mid-gut, and often remain attached when the head is cut off, thus rupturing the salivary ducts as well as the oesophagus, in the method of dissection just described. To obtain both pairs with certainty, however, a much more laborious method of dissection must be resorted to. The abdomen should be opened as described above, by lateral incisions, but instead of making the transverse cut about the middle of the abdomen, it should be made as far forward as possible. The ventral wall of the thorax should then be dissected off by continuing the lateral incisions forwards, and removed in pieces with the attached muscles, from the neck to the junction with the abdomen. The kidney-shaped glands then come into view, and by traction on the gut, which has already been exposed, the ducts leading to the tubular glands can be shown up. The rest of the dissection consists in freeing the structures required from the adherent fat body and the specialised cells described as occurring in this region. The appearance of a cleaned dissection is that of figure 1 on Plate LXX.

For the isolation of these structures a good binocular microscope is a necessity.

The two pairs of salivary glands and the first part of the mid-gut can sometimes be obtained by simply cutting through as much as possible of the integument at the neck and then pulling off the head by a slow and steady pull. This is, however, a very uncertain method, as the oesophagus and the ducts often break off in their passage through the mass of muscle, and once this method has been begun it is almost hopeless to attempt to find the structures by further dissection.

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CHAPTER VIII

THE ORDER ACARINA: IXODIDAE OR TICKS

THE Acarina or Acarians—often loosely spoken of as Acari or Mites—compose one of the largest and most important orders of the Phylum Arthropoda. They are closely related to the Spiders and Scorpions, especially to the Solpughids, large spider-like arthropods popularly known in India as 'jerrymungulums'.

In addition to many Acarians which cause troublesome skin diseases (acariasis) of animals, there are more than 200 species, belonging to the family Ixodidae or ticks, which are entirely blood-sucking in habit; no less than eighteen species of these are known to transmit pathogenic parasites to man and the domesticated animals. The order Acarina also includes a number of blood-sucking mites or acari, which, except for a few parasitic on rodents, have been very little studied. The mites which cause damage to crops and stored provisions are, however, much better known. The 'Harvest Mite', 'Harvest Bug', 'Rouget', or 'Red Flea', the well-known *Trombidium holosericeum*, is familiar in the harvest season in Europe and England. In the tropics, particularly during the rainy season, the worker may encounter numbers of the large 'Plush' or 'Velvet mite', another species of *Trombidium*. During the course of breeding experiments with Diptera, many species of mites parasitic on *Musca*, *Stomoxys*, *Philaematomyia*, *Psychoda* and mosquitoes are met with. In Madras it is not uncommon to find a specimen of *Philaematomyia insignis* with a dozen or more mites fixed to various parts of its body. In some cases these arthropods greatly interfere with breeding experiments; very little is known as to what effect they may have on their hosts.

For the most part Acarians are of small size. The body is compressed dorso-ventrally, seldom elongated, and shows no distinct head, thorax or abdomen; in a few forms the head and thorax (*cephalothorax*) is separated from the body by a groove or furrow; the body may or may not be covered by a chitinous plate the *dorsal shield* or *scutum*. At the anterior end of the cephalothorax there is a well-marked depression known as the *camerostoma*, into which the mouth parts are inserted; the latter are often spoken of

General structure: The mouth parts

collectively as the *rostrum* or *beak*, and may either project beyond the camerostoma or lie concealed below its dorsal wall, which is called the *epistoma*. The mouth parts consist of a pair of *mandibles* situated dorsally, which may either be armed with teeth or claws or may be styliform; they are often enclosed in sheaths covered with minute spines. The *maxillae* are situated ventrally and are usually shorter than the mandibles; they are narrow flat blades of chitin. Situated in the middle line of the ventral surface of the rostrum there is a flat rod of chitin, the *hypostome*, which is armed with teeth. In many acarina, as for instance the ticks, the maxillae are wanting, and it is generally believed that the hypostome, which in this case is well developed, represents the fused maxillae; hence the origin of the term *labio-maxillary dart*, which is often applied to it.

The palps

The palps consist of at most five joints, the terminal one of which is often armed with sensory hairs. Banks groups the various forms of palpi as follows:—'(1) Where they are simple, 'filiform and have a tactile function; (2) where they 'are modified for predatory purposes, being provided with spines, hooks 'or claws; (3) where the last joint is opposable to the preceding, so that 'the mite may by its palpi cling to some object; (4) where they have 'become obsolete, and are more or less united to the rostrum'.

Legs

The adult acarian has four pairs of legs, as also the nymph, but the larva has only three pairs. Banks states that in the embryo of *Gamasus* there are four pairs of legs before birth, one of which is aborted but develops again later at the nymphal stage; this, as he points out, shortens the gap between the Acarina and the Arachnida. Each leg consists of from five to seven segments as follows:—coxa, femur, tibia, protarsus and tarsus; sometimes a trochanter and patella may be recognized. Each leg is articulated either directly into the skin or into special skeletal enlargements spoken of as *epimera*. The tarsus ends either in one or three *claws* or *ungues*, and the number of these may vary in the different stages; they are seldom toothed. All the joints may be smooth or covered with hairs and spines; the latter often afford valuable taxonomic characters. At the base of the claw there is usually a pad-like sucker, the *pulvillum*, *caroncle* or *ambulacrum*, which is often rudimentary. In some acarians the first pair of legs have a peculiar sensory organ on the tarsus.

Eyes may or may not be present; when present they are as a rule situated either at the margin of the anterior end of the scutum, or on folds on the ventral surface.

Stigmata

The *stigmata* or external openings for the tracheae are usually situated on thickened plates of chitin, and may either be single or in pairs. In most of the terrestrial and aquatic acarians the stigmata are situated at the sides of the body and can easily be recognized with a hand lens. In the majority of the permanently parasitic forms stigmata are wanting and respiration is carried on through the skin. In many mites each stigma has a curious forward prolongation of a tubular nature, which is known as the *peritreme*; its function is unknown.

Reproduction

In all the acarians the sexes are distinct. The males are as rule smaller than the females and are often difficult to find; in many cases they never attach themselves to the host on which the female is parasitic. The reproductive organs open on the ventral surface close to the mouth parts. The male opening (*epiandrum*) is as a rule smaller than that of the female (*epigynum*), which is generally a large slit guarded by flaps or valves. Copulation is peculiar, as the mouth parts of the male are made to serve the purpose of a copulatory organ. They are inserted into the genital opening of the female, and as the bag of sperms (*spermatophore*) is passed out from the male sexual opening it is pushed into the female orifice by the mouth parts. In the case of the parasitic forms copulation may take place either on the host or away from it, the male awaiting the replete female. There are various secondary sexual differences to be noted, such as certain plates and shields and the shape of the dorsal scutum.

CLASSIFICATION

The classification of the Acarina is at present in an unsatisfactory state, as no common agreement has been reached by workers on this subject. As has been set forth in the introductory chapter, Ray Lankester divides the order Acarina into seven suborders according to the position of the stigmata. The Metastigmata includes the Ixodidae or ticks and the Gamasidae, and the latter together with three other suborders contains the mites which are of interest in the present connection. Of these the Prostigmata includes the Trombidiidae or Harvest mites, the Astigmata, the Sarcoptidae or Itch mites, and the Vermiformia the Demodicidae. Banks divides the order into several superfamilies, which are again divided into numerous families and genera. Another classification is that given by Neumann, which is here reproduced. This authority recognizes ten families, which he groups as follows:—

NEUMANN'S TABLE OF THE FAMILIES OF THE ACARINA.

Non-vermiform Acarina.	Legs inserted directly into the integument, without epimera.	Legs with 5 articles			**Oribatidæ.**
		Legs with 6 articles.	With tracheæ. Chelicerae.	provided with hooklets	**Ixodidæ.**
				didactylous or styliform	**Gamasidæ.**
			With no tracheæ (marine Acarina)		**Halacaridæ.**
	Legs articulated on distinct epimera.	Natatorial legs (aquatic Acarina)			**Hydrachnidæ.**
		Ambulatory Legs.	Cheliceræ styliform; palps free, antenniform		**Bdellidæ.**
			Cheliceræ styliform or in claws; palps free; predaceous		**Trombidiidæ.**
			Cheliceræ didactylous; palps cylindrical or conical, and partially adherent to the lips		**Sarcoptidæ.**
Vermiform Acarina		Legs with 5 articles			**Eriophyidæ.**
		Legs with 3 articles			**Demodicidæ.**

FAMILY IXODIDAE

Acarina with the abdomen compressed dorso-ventrally, unsegmented and completely fused with the cephalothorax; a pair of spiracles is situated in the posterior part of the body behind the last pair of legs. The capitulum articulates with the anterior end of the body and bears the rostrum or beak, which consists of the jointed palps (pedipalps), hooked mandibles lying in sheaths, and the fused maxillae forming the hypostome, which is armed with rows of recurved teeth simulating a rasp. The anus is situated ventrally in the posterior third of the body, and the sexual orifice in the anterior third. There are four pairs of legs, each consisting six joints or segments, terminating at their extremities in two curved claws and a ventral pad or pulvillum; the first pair contains a small fossette at its extremity known as 'Haller's organ', which is probably of a sensory nature.

Ticks in relation to disease: Natural Parasites

Of all the Acarina, the giant mites or ticks are the most familiar, and in tropical countries are to be found on almost every mammal. As is well known they are the transmitters of several species of the Piroplasmata and Spirochaetae, and the diseases which result from the invasion of the blood by these parasites are some of the most deadly which affect the domesticated animals. In 1893 Smith and Kilbourne proved by experiment that the cattle disease known as 'Texas Fever' is transmitted by a species of tick, *Margaropus annulatus*, Say, which they found on the sick animals. A considerable number of similar diseases are now known to affect other useful animals, such as the horse, mule, donkey and the dog; in the majority of instances the piroplasms which cause the diseases have been shown to be transmitted by different species of ticks.

The piroplasm of cattle, *Piroplasma bigeminum*, the cause of 'Texas Fever' in America, is common in tropical and subtropical regions. In the United States the parasite is transmitted by *Margaropus annulatus*, and in South Africa by *Rhipicephalus capensis*, Koch, C. L. In Europe, *Ixodes ricinus* is the probable transmitter, while in England *Haemaphysalis punctata*, Can. and Fan., has been experimentally proved by Stockman to be the carrier of this piroplasm. In South India the senior author has transmitted *Piroplasma bigeminum* to calves by *Margaropus annulatus*. In South America, Cuba, Porto Rico and the Philippine Islands *Margaropus annulatus*, variety *australis*, Fuller, is the carrier.

Theileria parva, a small species of piroplasm which is the cause of the cattle disease known as 'Rhodesian Fever,' is transmitted by *Rhipicephalus appendiculatus*, Neum. Theiler has recently shown that a new parasite of the red blood cells of cattle, which he names *Anaplasma marginale*, is transmitted by *Margaropus annulatus* variety *decoloratus*, Koch, C. L.

Dogs of all kinds and in many parts of the world are commonly attacked by a species of piroplasm, *P. canis*, which in South Africa is transmitted by *Haemaphysalis leachi*, Audoin, in India by *Rhipicephalus sanguineus*, Latr., and in Europe probably by *Ixodes ricinus*, L., and *Dermacentor reticulatus*, Fabr.

In South India the jackal is naturally infected with another species of piroplasm, *P. gibsoni*, which is probably also transmitted by a tick, though the effective species has not yet been determined; this parasite is exceptional in that it is not restricted to one vertebrate host but can be transmitted to the dog; it causes serious epidemics among the hounds of the Madras Hunt.

The disease of horses, mules and donkeys known as 'Biliary Fever' is caused by one or more species of Piroplasmata; in South Africa one of these parasites, *P. equi*, is carried by *Rhipicephalus evertsi*, Neum., and in Russia by *Dermacentor reticulatus*. In Europe *Piroplasma ovis*, the cause of 'Redwater' in sheep, is transmitted by *Rhipicephalus bursa*, Can. and Fan. In South Africa goats and sheep are known to suffer from a fatal disease called 'Heartwater' and although the parasite is unknown, it has been proved to be carried by *Amblyomma hebraeum*, Koch, C. L. The virus (parasite ?) of the human disease known as ' Rocky Mountain Fever ' is known to be transmitted by *Dermacentor andersoni* (*venustus*), Stiles.

In addition to the above diseases, ticks also transmit several of the *Spirochaetae*. *Spirochaeta duttoni*, the parasite of ' African Relapsing Fever,' is transmitted by *Ornithodorus moubata*, Murray ; *S. theileri*, another spirochaete found in the blood of cattle in South Africa, is carried by *Margaropus annulatus*, variety *decoloratus*. *Spirochaeta marchouxi*, which causes spirochaetosis in fowls, is transmitted in nature by *Argas persicus*, Fisch-Wald.

Certain species of ticks are believed to be the invertebrate hosts of mammalian and reptilian haemogregarines. Christophers has described the sexual cycle of *Leucocytogregarina canis* in the alimentary tract of *Rhipicephalus sanguineus*. In this case the sporozoits are not found in the salivary glands of the tick, but remain in a cyst in the alimentary tract ; probably they regain the vertebrate host when the dog eats the tick, the sporozoits being liberated by the action of the digestive fluids on the cyst wall ; this has, however, not been proved for the haemogregarine of the dog. Certain haemogregarines of frogs and lizards are believed to undergo their sexual cycles in ticks parasitic on their hosts.

A few ticks are naturally infected with flagellates of the genus *Crithidia*. In Madras *Rhipicephalus sanguineus* is infected with *Crithidia christophersi*, Novy, and *Haemaphysalis bispinosa* with *Crithidia haemaphysalidis*, Patton. These two flagellates are of peculiar interest as they are transmitted hereditarily. Bishop has also recorded a flagellate from *Ixodes ricinus* in England, and O'Farrel a *Crithidia* from *Hyalomma aegyptium* in the Soudan.

EXTERNAL ANATOMY *

(Plates LXXII and LXXIII)

Capitulum
Plate LXXIII

The body of a tick is oval or elliptical in contour, flattened dorsoventrally, the dorsal surface being gently convex ; there is no distinct cephalothorax demarcated off from the rest of the abdomen, but the two are fused together to form the body. Fixed into a special opening, the *camerostoma*, is the *capitulum* (*rostrum*), often erroneously spoken of as the head ;

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* The account of the external anatomy given here applies only to the Ixodini, such as any common species of *Hyalomma* or *Rhipicephalus*. The important external characters of the Argatini are noted on page 580.

PLATE LXXII

Figure	1.	Dorsal view of *Hyalomma aegyptium*, ♂.	× 20.
Figure	2.	Dorsal view of *Amblyomma crenatum*, ♂.	× 15.
Figure	3.	Ventral view of *Hyalomma aegyptium*, ♂.	× 20.
Figure	4.	Dorsal view of *Ornithodorus savignyi*, ♀.	× 6.
Figure	5.	Dorsal view of same.	× 6.
Figure	6.	Dorsal view of *Aponomma gervaisi*, ♀.	× 17.

Reference Letters

ac.p.	Accessory plate.	hy.	Hypostome.
ad.p.	Adanal plate.	L 1.	Leg I.
a.g.	Anal groove.	L 2.	Leg II.
an.	Anus.	L 3.	Leg III.
ca.	Capitulum.	L 4.	Leg IV.
cam.	Camerostome.	l.g.	Lateral groove.
ca.p.	Caudal process.	mg.	Median groove.
c.g.	Cervical groove.	mn.	Mandibles.
cl.	Claws.	p.	Palps.
cx. i.	Coxa I.	pl.	Pulvillum.
cx. ii.	Coxa II.	plg.	Postero-lateral groove.
cx. iii.	Coxa III.	psa.	Pseudo-articulation.
cx. iv.	Coxa IV.	pts.	Protarsus.
cx.f.	Coxal fold.	sc.	Scutum.
e.	Eye.	scx.f.	Supracoxal fold.
f.	Femur.	sp.	Spiracle.
fs.	Festoons.	tb.	Tibia.
g.a.	Genital aperture.	tr.	Trochanter.
g.g.	Genital groove.		

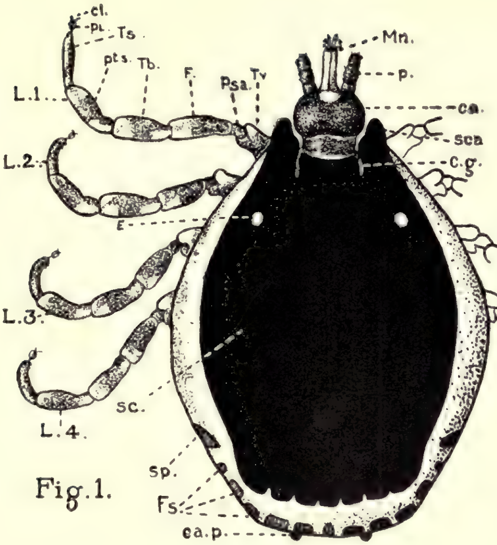
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Fig. 1.

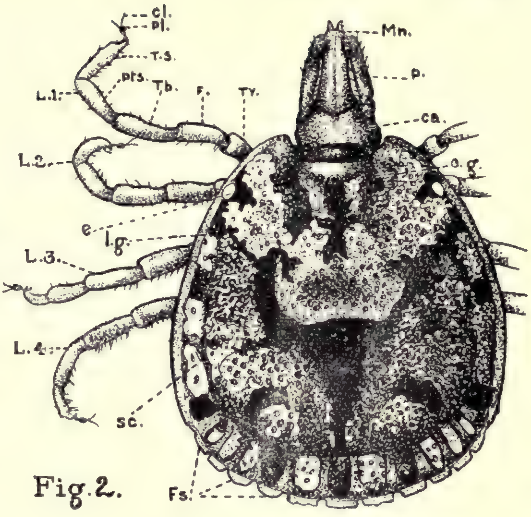
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Fig. 2.

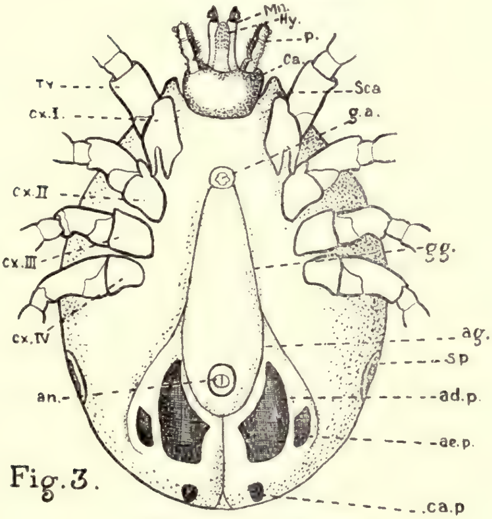
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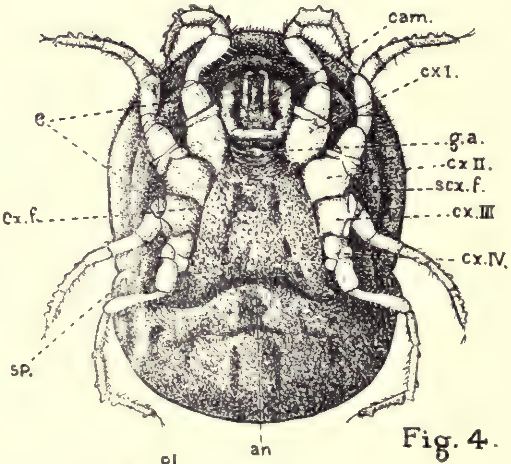
Fig. 3.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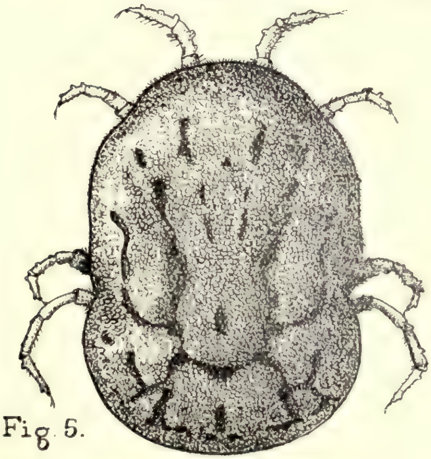

Fig. 5.

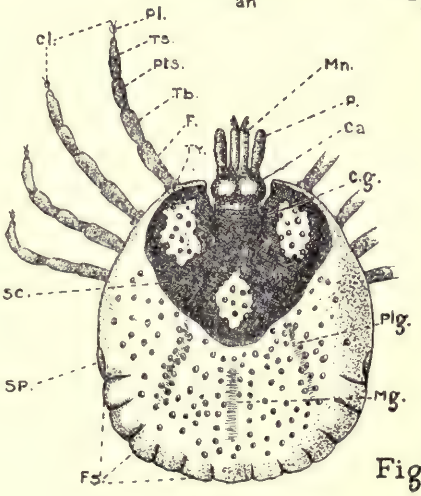
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Fig. 6.

the true head of a tick is not recognizable, as it has become fused with the rest of the body. The capitulum is the small chitinous structure which bears the mouth, and which has attached to it several specialized appendages. It consists of the following parts:—

The *basis capituli*, or mouth shield, is the dense basal portion which articulates with the body by a broad neck-like structure; when viewed dorsally it is more or less flattened and rectangular in shape; its ventral surface is usually convex. The shape of the basis capituli varies in different species, and is of some taxonomic value; it may, for instance, be triangular, globular, or hexagonal. The postero-lateral margins may be prominent as in the case of *Rhipicephalus sanguineus* (Plate LXXVII, figs. 1 and 2) or they may be rounded off (Plate LXXIII, fig. 10). On the dorsal surface of the basis capituli there is a well-marked ridge, the *dorsal ridge* (Plate LXXIII, figs. 1, 4, 5, 8, 10, 11, 13 and 14), which extends transversely across the dorsum up to the postero-lateral margin, where it may end. The ridge comes in contact with the anterior edge of the scutum, especially when the capitulum is raised; the posterior portion of the basis capituli is then concealed.

On the dorsal aspect on each side of the central area there is a shallow depression which contains the *porose areas* (Plate LXXIII, figs. 1, 4, 8, 10 and 14); these structures, which are present only in the female, consist of many minute open pores; they are of considerable taxonomic value. In the male tick the dorsal surface of the basis capituli is much smoother, there being no porose areas, and the ridges, except the dorsal one, are poorly developed. There are, however, a few scattered pores to be seen, and occasionally a few hairs, when the basis capituli is said to be *glabrous*.

Palps

Deeply embedded into the antero-lateral margins of the basis capituli, in some species towards the ventral side, in others towards the dorsal, there are two flap-like structures, the *palps* (Plate LXXIII, all figs.) which vary considerably in shape and size in the different species of ticks; the general outline, however, is that of a truncated cone. In *Hyalomma* (Plate LXXIII, figs. 4 and 5) they are long and valvate, partially obscuring the mouth parts; in *Haemaphysalis* (figs. 11 and 12) and *Rhipicephalus* (fig. 9) they are short and broad, while in *Ixodes* (figs. 1 and 2) they are long and cone-shaped. Each palp consists of four segments, which differ considerably in size and form. Each has a dorsal, a ventral, an external and an internal or median surface, and these vary in the different genera. The first (basal or proximal) segment is nearest to the basis capituli; it is usually small and nearly always hidden when the palps are examined from the dorsal surface; ventrally this segment is seen as a small knob. It is best studied in specimens in which the capitulum has been removed and cleared in caustic potash solution. The second segment is usually the longest and most prominent, and with the third forms more than half the total length of the palp; it varies much in shape. In *Hyalomma* (Plate LXXIII, fig. 5) it is long and deeply scooped out, and is markedly convex on its external surface. The third segment is generally smaller than the second, and is often deeply excavated on its median surface; on the inner side of its distal end it has a hollow into which the fourth segment (Plate LXXIII, figs. 2, 3, 5, 6, 7, 9, 11, 12, 13 and 15) is inserted. This latter is always small and bears a certain number of sensory hairs. The second and third segments, when deeply excavated, ensheath and protect the mandibles and hypostome. On their internal margins these segments are often armed with peculiar feathery hairs, the number and arrangement of which are of some importance in the identification of the species. The other surfaces usually have pores and simple hairs.

Mandibular sheaths and mandibles

The paired *mandibular sheaths** (Plate LXXIII, figs. 8, 10 and 14), with their contained *mandibles* or *chelicerae*, are the next structures of importance to note. Each sheath is continuous with the anterior portion of the basis capituli, and lies in close contact with its fellow of the opposite side. At its distal or free extremity the sheath forms a thin membrane which is invaginated and attached to the shaft of the mandible, so that the two move together. The outer surface of the sheath, except in its proximal third, is covered with minute denticles arranged in rows close to each other, giving the surface the appearance of a file. Each *mandible* (Plate LXXXV, figs. 8 and 9) consists of a cylindrical bar of chitin, the *shaft*, which in a partially cleared tick may be seen to project into the body cavity for a considerable distance below the base of the capitulum. Its dilated and proximal portion forms the *bulb*, which is specially grooved to allow space for the attachment of the retractors and extensors of the mandible. The shaft is cylindrical in shape with a ridge on its median surface, and is thickened at its distal end to allow of the articulation of the digits. Each *digit* (Plate LXXXV, figs. 8 and 9) is an irregularly shaped piece of chitin articulating with the end of the *shaft* of the mandible, and consists of two moveable articles. The large internal one, which is continued forwards into a long hooked tooth

* The sucking apparatus is described in the section dealing with the internal anatomy.

PLATE LXXIII

Types of Capitula

Figure 1. Dorsal view of capitulum of *Ixodes angustus*, ♀.

Figure 2. Ventral view of capitulum of same.

Figure 3. Ventral view of capitulum of *Aponomma pattoni*, ♀.

Figure 4. Dorsal view of capitulum of *Hyalomma aegyptium*,

Figure 5. Ventral view of capitulum of same.

Figure 6. Ventral view of capitulum of *Dermacentor andersoni* (*venustus*), ♀.

Figure 7. Ventral view of capitulum of *Margaropus annulatus*, ♀.

Figure 8. Dorsal view of capitulum of same.

Figure 9. Ventral view of capitulum of *Rhipicephalus haemaphysaloides*, ♀.

Figure 10. Dorsal view of capitulum of *Amblyomma americanum*, ♀.

Figure 11. Ventral view of capitulum of *Haemaphysalis bispinosa*, ♀.

Figure 12. Ventral view of capitulum of *Haemaphysalis leachi*, ♀.

Figure 13. Ventral view of capitulum of *Amblyomma americanum*, ♂.

Figure 14. Dorsal view of capitulum of *Amblyomma testudinarum*, ♀.

Figure 15. Ventral view of same.

Reference Letters

1 a.	First palpal segment.
2 a.	Second palpal segment.
3 a.	Third palpal segment.
4 a.	Fourth palpal segment.
D.r.	Dorsal ridge.
Hy.	Hypostome.
M.	Mandible.
M.s.	Mandibular sheath.
P.a.	Porose area.
Sc.	Scapula.
T.	Teeth.

PLATE. LXXIII.

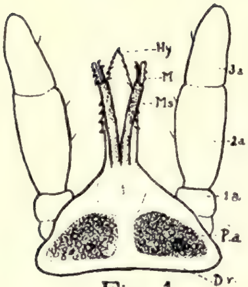
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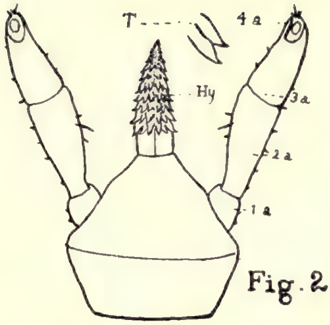
Fig. 1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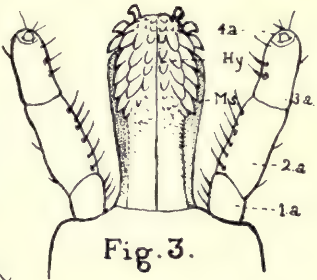
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Fig. 3.

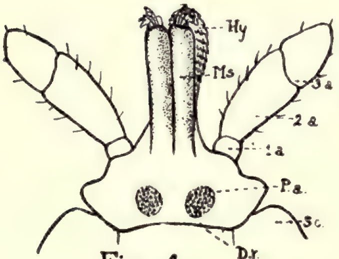
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Fig. 4.

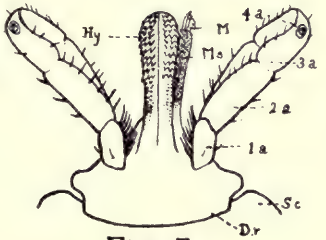
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Fig. 5.

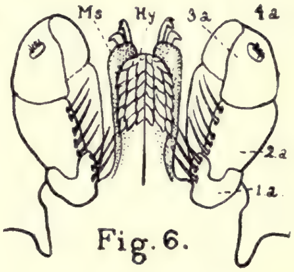
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Fig. 6.

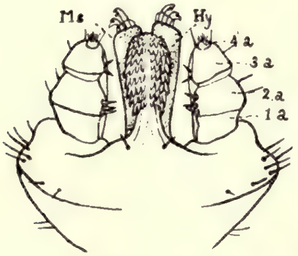
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Fig. 7.

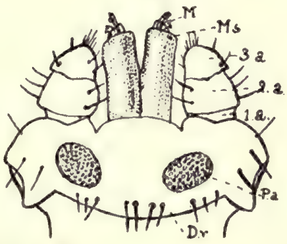

M
Ms
3a
2a
1a
Pa
Dr

Fig. 8.

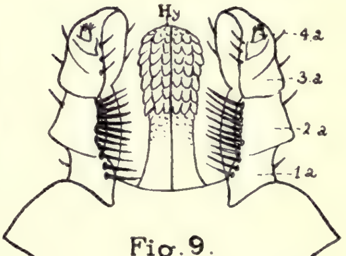

Hy
4a
3a
2a
1a

Fig. 9.

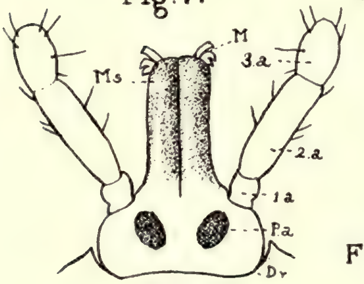

M
Ms
3a
2a
1a
Pa
Dr

Fig. 10.

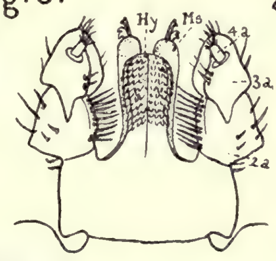

Hy
Ms
4a
3a
2a

Fig. 11.

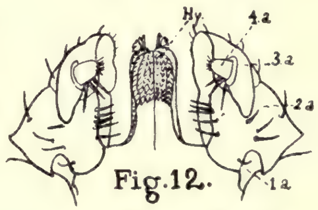

Hy
4a
3a
2a
1a

Fig. 12.

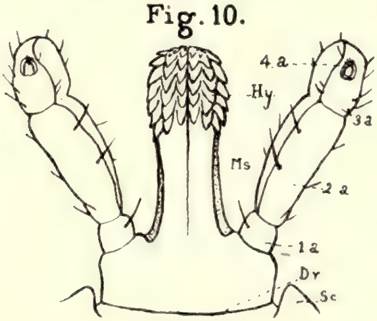

4a
Hy
3a
Ms
2a
1a
Dr
Sc

Fig. 13.

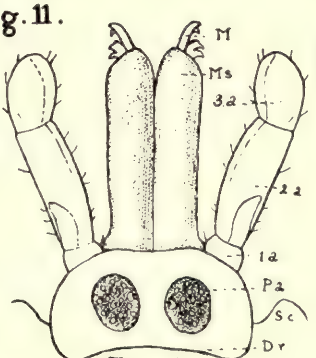

M
Ms
3a
2a
1a
Pa
Sc
Dr

Fig. 14.

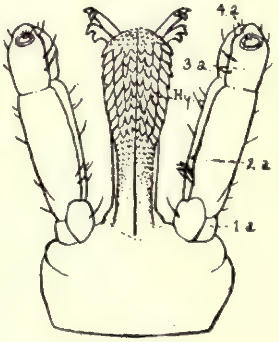

4a
3a
Hy
2a
1a

Fig. 15.

directed backwards, has attached to it a *dorsal process* (Nuttall and Warburton) which consists of one or more teeth. The external article, which may consist of three or more teeth, articulates with the outer side of the internal article. The whole digit can be retracted or extended by the action of the retractor and extensor muscles which are attached to the bulb of the mandible. The teeth vary in size, shape and number in the different species; they are not of very great taxonomic value.

Hypostome

The *radula*, *hypostome* or *labio-maxillary dart* (Plate LXXIII, figs. 1, 2, etc.; Plate LXXXV, figs. 6 and 7) is the most prominent structure on the ventral surface of the capitulum. It is an elongate, spatulate piece of chitin arising from the basis capituli between the palps, and is composed of two symmetrical halves which bear a number of small teeth with their points directed backwards; these are arranged in rows, those on one half corresponding with those on the other, forming regular transverse rows. The rows of teeth vary in the different species, as regards the number and the size and shape of the individual teeth. In many ticks the hypostome is armed with teeth from its tip to its base, while in others they are only present on the distal two-thirds, the remaining portion being smooth. The extremity of the hypostome is often covered with a large number of minute teeth crowded together in an irregular manner; it is then spoken of as having a *corona* (Nuttall and Warburton).

Scutum

In the male (Ixodini) the *scutum* covers the whole of the dorsal surface (Plate LXXII, figs. 1 and 2), in the female only about the anterior half (fig. 6). It is the chief characteristic of the Ixodini, and is absent in the Argatini (Plate LXXII, fig. 5; Plate LXXIV). The scutum is a hard chitinous plate of varying shape; it may be heart-shaped, oval, or more or less rounded (see figs.). Its anterior end may be emarginate or deeply hollowed out; the lateral angles in certain species are prolonged into well-defined shoulders, the *scapulae* (Plate LXXII, figs. 1 and 2), which project on each side of the basis capituli. The scutum may be highly ornamented and the colouring is distributed either in an irregular manner (Plate LXXII, fig. 2; Plates LXXIX and LXXX), or collected together to form spots (Plate LXXII, fig. 6); the surface of the scutum is always more or less punctate (Plate LXXII, figs. 2 and 6), and may or may not possess hairs. The colour designs and spots are well marked in certain species of *Amblyomma*, *Dermacentor* and *Aponomma* (see figs.) but in the majority these designs should not be entirely depended on for identification; they vary in their arrangement in different specimens and are apt to fade when the tick is kept in alcohol.

Eyes

Situated at the lateral margins of the scutum, either on the edge or just inside it, there are two small globular protuberances, the *eyes* (Plate LXXII, figs. 1 and 2); they may be of a light yellowish colour or dark brown. In some species they are more or less flattened and inconspicuous, while in others they appear as buttons sunk into small pits. Eyes are present in certain genera and absent in others; as they can be readily seen with a good hand lens their shape, size and position are of some taxonomic importance.

Dorsal porose areas

About the centre of the scutum of the male, and just posterior to it in the female, there are two spots, the *dorsal porose areas* or *foveae*. When examined with a high power they are seen to consist of a number of small protuberances, each of which has a pore at its summit; they occur in both sexes when present in the species, and have been described from several genera (*Dermacentor, Rhipicephalus, Margaropus* and *Hyalomma*). Their function is unknown, but they are probably sense organs.

Grooves and furrows, Plate LXXII

Cervical groove (figs. 1, 2 and 6) is the name applied to the furrows which extend backwards from the inner angles of the scapulae towards the posterior margin in both sexes. The *lateral groove* (fig. 2) extends along the side of the scutum in both sexes; in the male it often reaches the posterior margin. The *marginal groove* runs along the side of the body of the female. *Median* and *postero-lateral furrows* (fig. 6) are the names given to certain ill-defined depressions near the posterior borders in the males and females of certain species; they are not, however, of much importance, as they alter in shape when the tick is replete with blood and during muscular contraction. The *marginal* or *postero-marginal festoons* (figs. 1, 2 and 6) are usually eleven in number, and are best seen in the males and unfed females. They are small chitinous plates bounded by furrows, and give the posterior margin of the body of the tick a festooned appearance.

Ventral surface of body genital aperture and grooves

On the ventral surface of the body the following structures should be noted:—Genital aperture, ventral shields, anal aperture, ventral and anal plates, stigmata or spiracles, legs, furrows, grooves and pits. The *genital aperture* (Plate LXXII, fig. 3) lies in the median line towards the anterior end and just behind the basis capituli; it will be readily recognized as a transverse slit, guarded anteriorly by a chitinous flap, the *apron*, and posteriorly by a raised margin of the ventral integument. Extending from each side of the genital orifice there are two well marked grooves, the *genital grooves* (fig. 3), which pass backwards and outwards to the posterior margin of the body; these furrows are of some importance in the identification of species. The *anal orifice* (fig. 3) is situated in the median line posterior to the last pair of legs; it consists of a longitudinal slit which is guarded by two lateral chitinous valves. The groove which surrounds the anus is of great importance in the grouping of the several genera, as it varies in its position and shape. In the genus *Ixodes* (Plate LXXVI, figs. 1, 5 and 6) it surrounds the anal aperture anteriorly, its two arms extending backwards in a divergent, convergent or parallel direction, towards the posteior margin. In several species of the *Ixodes*, however, the anal groove instead of being rounded anteriorly is pointed like a gothic arch; it is then spoken of as being *ogival* (Nuttall and Warburton). This type of anal groove is seen for instance in the species *Ixodes minor*, Neum., *Ixodes sculptus*, Neum., and others. In the genera *Haemaphysalis*, *Dermacentor*, *Hyalomma*, *Amblyomma* and *Aponomma* (see figs.) the anal groove, instead of extending around the anal opening anteriorly, curves round it posteriorly, the two limbs then passing forwards towards the genital grooves, with which they often unite. In the genus *Margaropus* (see figs.) the anal groove is obsolete, and it is here that the classification of the genera based on the position of the anal groove breaks down. On the ventral surface of many ticks a distinct *postero-median groove* is frequently present, and may be united with the anal groove; this median groove extends to the posterior end of the body.

Anal orifice and groove

In the males of certain species of ticks there are flat pieces of chitin, the *ventral plates*, embedded in the skin and either slightly or considerably raised above the surface; they are of great importance in the identification of species. In the genus *Ixodes* (Plate LXXVI, fig. 1) there is a *pregenital plate* situated in front of the genital orifice, a *median plate* lying between the genital and anal openings, and an *anal plate*, in the median line, on which the anus is situated. An *adanal plate* lies on each side of the anal plate, and the two may unite behind it near the posterior border. The *epimeral plates* lie outside the genital grooves, extending backwards towards the fourth legs. Any or all these plates may be absent, as in the genera *Dermacentor* and *Haemaphysalis*.

Ventral plates, plaques, shields and caudal appendage

Plaque is the name given to a small piece of chitin situated on the posterior margin of the ventral surface, just anterior to the festoons; plaques are present in certain species of *Amblyomma*. ***Shields*** are prominent raised plates of chitin ending in points, and are as a rule situated on each side of the anal aperture in the males of the genera *Hyalomma*, *Margaropus* and *Rhipicephalus* (see figs.) These shields are divided into two groups, the ***adanal***, which are always present close to the anus, and the ***accessory***, external to the adanal. In the males of the genus *Margaropus* there is often a ***caudal appendage***, which projects from the posterior border and is best seen when the tick is somewhat distended with blood; in the male of *Hyalomma aegyptium* (Plate LXXII, fig. 3) there are two such appendages, one on each side, which end in chitinised points.

Legs. Plate LXXII

Adult ticks always have four pairs of legs, as also have the nymphs, but there are only three in the larva. Each leg is composed of six segments, which are united to each other by intersegmental membranes, the usual method of articulation in the Arthropoda. The *coxa* or basal segment is immovable, and is often armed with a single spur, when it is said to be ***dentate***; or it may be armed with two spurs with a deep incision between them, when it is said to be ***bidentate***. The next segment, the ***trochanter***, is shorter and may be broader than it is long. The ***femur*** is much longer and is jointed to the trochanter by a pseudo-articulation. The fourth segment or ***tibia*** and the fifth or ***protarsus*** are also elongated. The sixth segment or ***tarsus*** may also form a pseudo-articulation at its proximal end; at its extremity there is either a long or a short stalk, to which are attached two well-developed claws. In the Ixodini the tarsi are nearly always armed with one or more ventral spurs; their presence or absence, and the manner in which the tarsi end, are of importance in distinguishing the species. In the Argatini the tarsi are never armed with spurs. On the ventral surface of the claws there is a disc-like expansion, the ***pulvillum***, which is well developed in the Ixodini, but is rudimentary or absent in the Argatini; the length of the claws and that of the pulvillum in relation to them should be noted.

Hallers organ: Spiracle

On the first pair of tarsi there is a remarkable structure known as 'Hallers organ'; it consists of several cup-shaped pores containing sensory hairs and dermal cells, and is situated on the dorsal surface of the tarsus. It has been fully described by Nuttall in collaboration with Cooper and Robinson; according to Lahille and others its function is olfactory.

The ***spiracles*** or ***stigmal plates*** are seen as small raised plates of dark brown chitin ; they lie ventro-laterally one on each side behind coxa IV. In the Argatini they are situated between legs III and IV. Each spiracle may be circular, oval, triangular or comma-shaped ; its size, shape and structure is of importance in the separation of genera and species. It is more fully described further on.

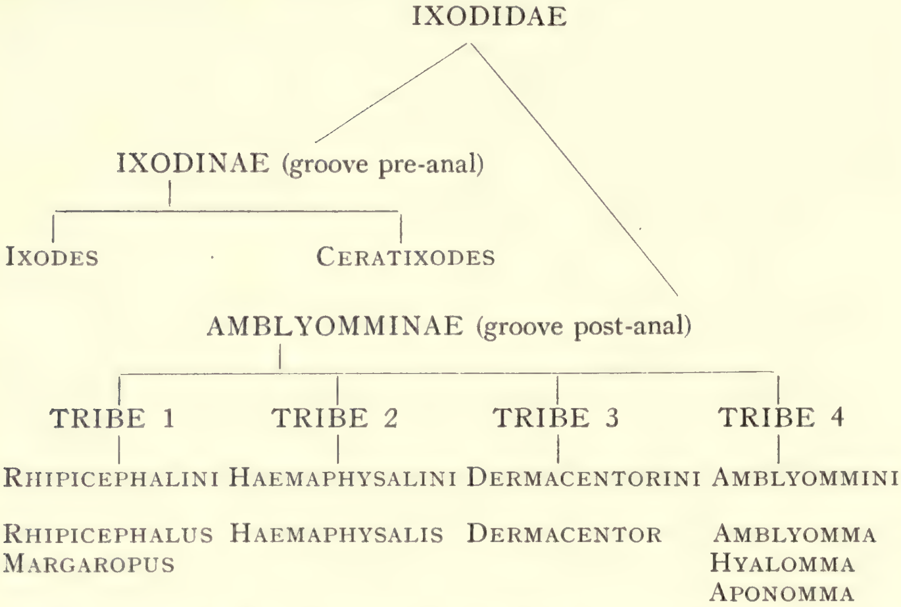
CLASSIFICATION

The classification of ticks has attracted the attention of many zoologists, and the literature of the subject is very extensive ; it is not possible in a limited space to review it in detail, and only the main points are given here. The worker will find a complete historical review of the subject of the classification of ticks in the *Monograph of the Ixodoidea*, Part II, by Nuttall in collaboration with Warburton, Cooper and Robinson.

According to Neumann ticks are placed in the family Ixodidae, which is divided into two subfamilies, the Ixodinae and the Spelaeorhynchinae. The subfamily Ixodinae contains two sections, the Ixodini and the Argatini, and these are further sub-divided into several genera, containing more than 200 species. The Argatini are widely separated from the Ixodini, and there are no intermediate forms known at present. The Argatini consists of a small number of specialized ticks which fall naturally into two genera as described below. The Ixodini, on the other hand, contains a large number of somewhat closely related species all of which have a dorsal shield or scutum, which is absent in the Argatini.

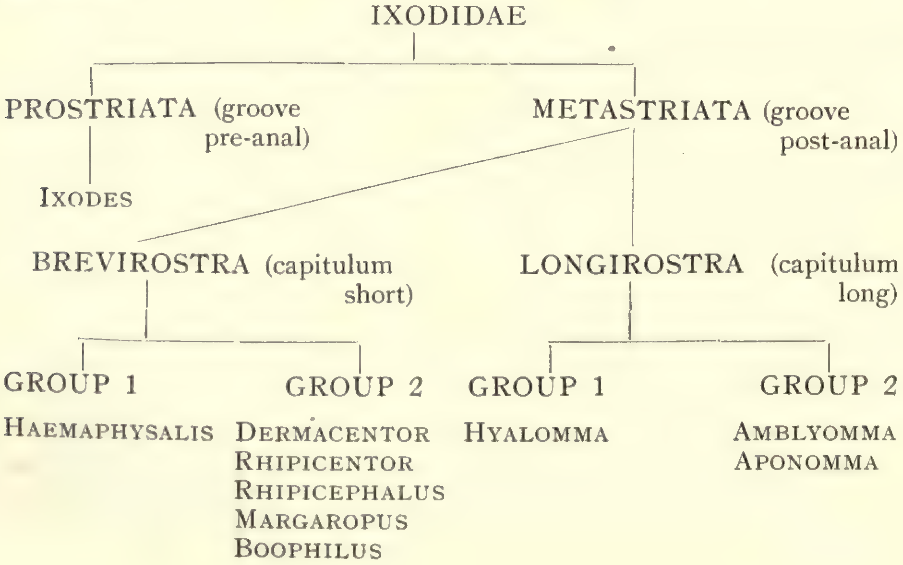
Many attempts have been made to arrange the Ixodini in natural groups. As a basis for the various methods of classification the relative length of the palps has been mainly utilized, as being an external feature which shows a difference in anatomical structure. Neumann has, however, pointed out that it leaves too much to the judgment of the observer, and also cuts across the real affinities existing between the various species. In 1902 he suggested that the grooves on the ventral surface of the Ixodini were good external features to select as a basis for classification ; since then Banks and Warburton have independently drawn up systems of classification depending on the position of the anal groove.

Banks places ticks in the superfamily Ixodoidea, which he divides into two families, Ixodidae and Argasidae ; the former he sub-divides as follows :—


IXODIDAE
IXODINAE (groove pre-anal)
IXODES
CERATIXODES
AMBLYOMMINAE (groove post-anal)
TRIBE 1
TRIBE 2
TRIBE 3
TRIBE 4
RHIPICEPHALINI
HAEMAPHYSALINI
DERMACENTORINI
AMBLYOMMINI
RHIPICEPHALUS
MARGAROPUS
HAEMAPHYSALIS
DERMACENTOR
AMBLYOMMA
HYALOMMA
APONOMMA

Banks believes that *Amblyomma*, *Hyalomma* and *Aponomma* are more nearly related to each other than to *Dermacentor*, and that *Dermacentor* is more closely related to *Amblyomma* than to *Rhipicephalus*.

Warburton also places ticks in the superfamily Ixodoidea, which he divides into the families Argasidae and Ixodidae; the latter he groups as follows:—


IXODIDAE
PROSTRIATA (groove pre-anal)
METASTRIATA (groove post-anal)
IXODES
BREVIROSTRA (capitulum short)
LONGIROSTRA (capitulum long)
GROUP 1
GROUP 2
GROUP 1
GROUP 2
HAEMAPHYSALIS
DERMACENTOR
RHIPICENTOR
RHIPICEPHALUS
MARGAROPUS
BOOPHILUS
HYALOMMA
AMBLYOMMA
APONOMMA

Neumann, whose opinion naturally carries great weight, places ticks in the family Ixodidae, which he divides into two subfamilies as noted above. The subfamily Ixodinae is distinguished from the subfamily Spelaeorhynchinae by the presence in the former of a well developed hypostome, which is armed with rows of recurved teeth; in the latter the maxillae are reduced to two small membraneous laminae, and the hypostome is styliform and without teeth. He sub-divides the Ixodinae into two sections, the Ixodini and the Argatini, and classifies the former as follows:—

IXODINI

TRIBE 1	TRIBE 2	TRIBE 3
IXODARIA	RHIPICEPHALARIA	AMBLYOMMATARIA
IXODES	RHIPICEPHALUS	AMBLYOMMA
CERATIXODES	MARGAROPUS	DERMACENTOR
ESCHATOCEPHALUS	HYALOMMA	APONOMMA
		HÆMAPHYSALIS

Neumann retains the genera *Ceratixodes* and *Eschatocephalus.* His genus *Margaropus* includes *Boophilus,* Curtice, and *Margaropus,* Karsch. He does not recognize the genus *Rhipicentor,* Nuttall and Warburton, and places the type species, *Rhipicentor bicornis* under *Rhipicephalus gladiger,* Neumann. The genus *Hyalomma* is placed along with *Rhipicephalus* and *Margaropus,* whereas Warburton keeps it in a group to itself; Banks places it along with *Amblyomma* and *Aponomma.*

In dealing with the genera and species Neumann's classification is adopted here; the keys and most of the descriptions are taken from his recent work on ticks, *Ixodidae,* in *Das Tierreich.* Part 26, 1911.

SECTION ARGATINI

Ticks without a scutum, the integument being leathery and covered with mammillae. Capitulum ventral in the nymphal and adult stages. Palps free and leg-like, the articles cylindrical. Spiracles usually small, and situated in front of coxa IV. Coxae contiguous or sub-contiguous. Tarsi with rudimentary or no pulvilli; sexual dimorphism slight. (Neumann)

General Structure
Plate LXXXIV.

The Argatini contains two genera, *Argas* and *Ornithodorus*, the species of which are characterised by the flat shape of their bodies and the ventral position of the capitulum; in the larval stage the latter may be terminal or sub-terminal. On the ventral surface of the adult there are two folds, one internal to the coxae, the *coxal fold*, and the other above the coxae, the *supracoxal fold*. The base of the capitulum is rectangular and is attached dorsally to the surface of the cephalothorax; the hypostome is broader at its base than at its apex, and is nearly always armed with a smaller number of teeth than is usually found in the Ixodini. The articles of the mandibles are more delicate than those of the Ixodini. The four segments of the palps are cylindrical and leg-like, and are all about the same length. The eyes, which are present only in some species of *Ornithodorus*, are arranged in one or two pairs situated in the supracoxal fold. The spiracles are discoidal or reniform in shape. The legs are of medium length and the coxae are always devoid of spurs; the tarsi and protarsi frequently have marked protuberances. The male is usually a little smaller than the female, otherwise they are much alike. The genital aperture in both sexes is situated in the interval between legs I and II. In the male it is narrow and almost as long as it is broad, and is semi-lunar in shape; in the female it is a wide transverse slit with more or less parallel borders; it is almost as broad as the base of the rostrum.

GENUS ARGAS, LATREILLE

Body flat, oval or rounded in contour, with a flattened margin giving it a sharp edge which is apparent even when the tick is replete with blood. The body is often narrowest in front and may even be pointed. The integument is not mammillated, but has on the dorsum and venter symmetrically arranged discs usually disposed in radial lines; the remainder of the skin is wrinkled into irregular folds. The coxal and supracoxal folds are prominent. Eyes are absent. (Neumann)

According to Neumann the genus *Argas* consists of nine well established species, one doubtful and two separated into four sub-species. He gives the following key for the identification of the species.

NEUMANN'S KEY TO THE SPECIES OF ARGAS

1.	Body at sides convex, without pointed anterior end	2
	Body at sides rectangular, parallel, with anterior end blunt	8
2.	Body oval, longer than broad, straighter anteriorly	3
	Body discoidal, or circular, broader anteriorly	**vespertilionis.**
		(France; England; Germany; Egypt; Algeria; S. India.)

PLATE. LXXIV.

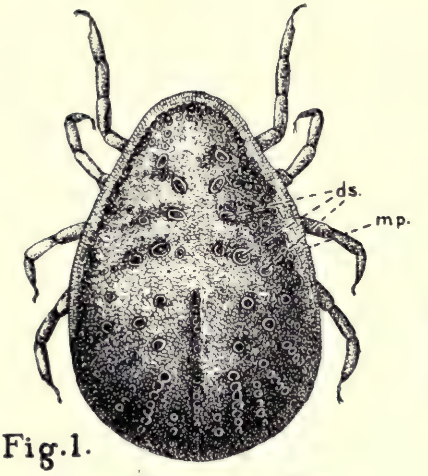


Fig. 1.

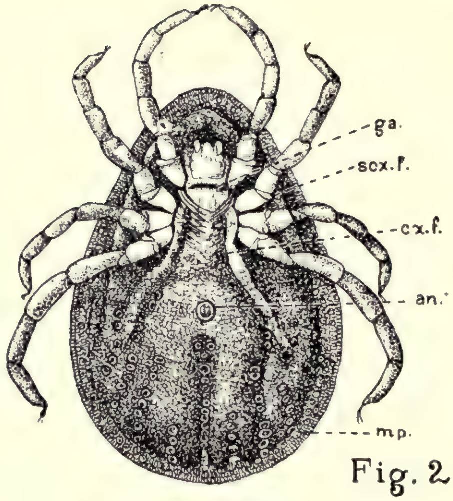

ga.
scx.f.
cx.f.
an.
mp.

Fig. 2.

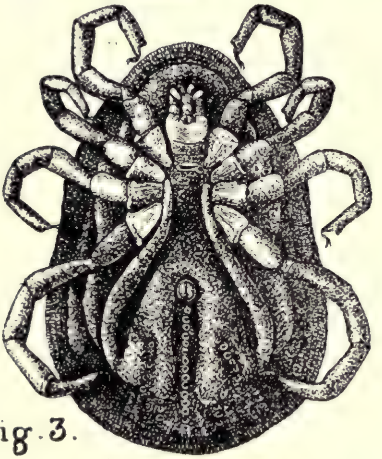


Fig. 3.

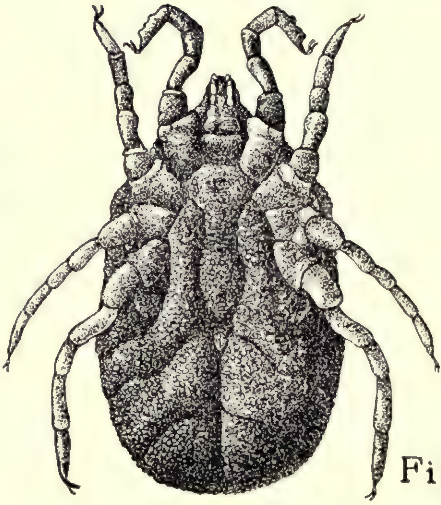


Fig. 4.

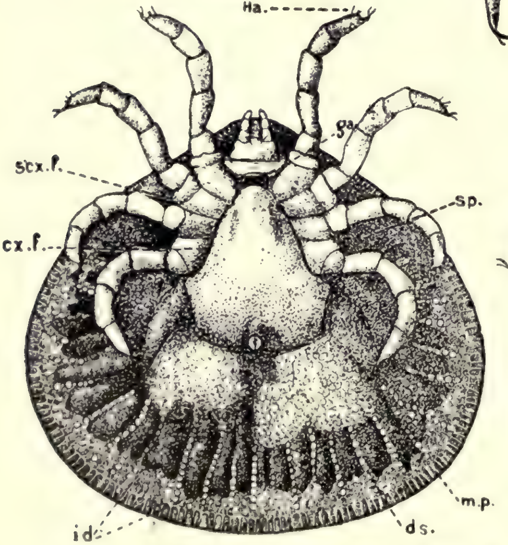

Ha.
ga.
scx.f.
sp.
cx.f.
m.p.
id.
ds.

Fig. 5.

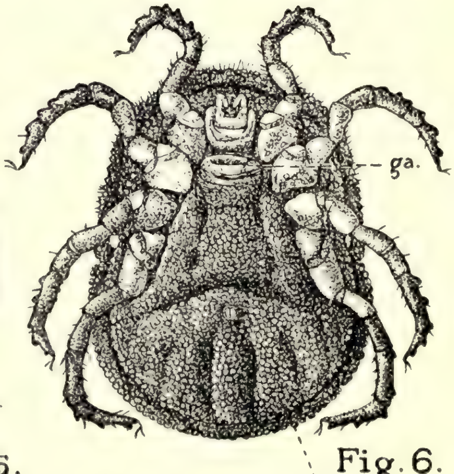
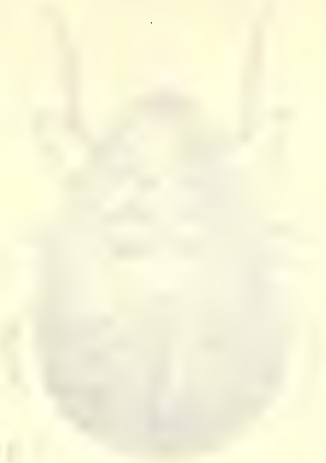


Fig. 6.

PLATE LXXIV

Figure 1.	Dorsal view of *Argas persicus*, ♀. ds., discs. mp., marginal pits. × 8.
Figure 2.	Ventral view of same. an., anus. cx.f., coxal fold. ga., genital aperture. mp., marginal pits. scx.f., supracoxal fold. × 8.
Figure 3.	Ventral view of *Argas reflexus*, ♀. Note the contiguous coxae and compare with figure 2. × 12.
Figure 4.	Ventral view of *Ornithodorus turicata*, ♂. × 12.
Figure 5.	Ventral view of *Argas vespertilionis*, ♂. cx.f., coxal fold. ds., discs. ga., genital aperture. Ha., Haller's organ. id., intestinal diverticula. scx.f., supracoxal fold. sp., spiracle. × 14.
Figure 6.	Ventral view of *Ornithodorus moubata*, ♀. ga., genital aperture. m., mammillae. × 6.

PLATE LXXIV



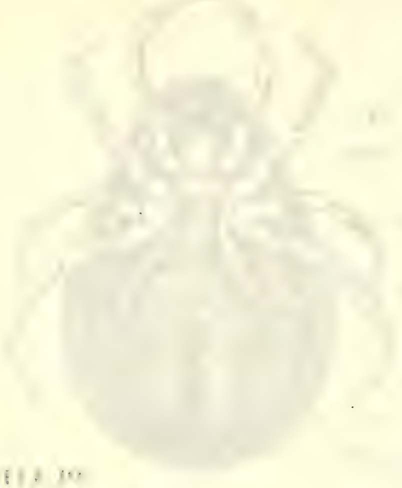


Fig. 3.

Fig. 4.

3. Body margin formed of straight folds 4
Body margin formed of rectangular folds . . . . . **persicus.**
(Asia; Persia; Turkestan; North and Central India; China; Africa; Egypt; Algeria; South Africa; Australia; Mauritius.)

4. Body flat, folds of integument distinctly marked 6
Body long and rounded, folds of integument delicately wrinkled 5

5. Discs of middle row nearly contiguous; tarsus IV four times as long as wide . . . . **hermanni.**
(Egypt; Abyssinia.)
Discs of middle row separated; tarsus IV five times as long as broad . . . . **delicatus.**
(Central Asia, Karachar.)

6. Body oval, narrower in front . . . . **reflexus.**
(Italy; France; Germany; Russia; Algeria.)
Body elliptical, broader anteriorly 7

7. Body twice as long as broad, base of rostrum narrower posteriorly . . . . **cucumerinus.**
(Peru.)
Body nearly as broad as long, base of rostrum rectangular, and considerably anterior to coxa I . . . . . . **transgariapinus.**
(South Africa; Orange Free State; Basali Land.)

8. Tarsi with no preungual dorsal protuberance . . . . . **aequalis.**
(German East Africa.)
Tarsi with prominent preungual dorsal protuberance . . . **brumpti.**
(Somaliland; Ogaden.)

Argas reflexus, Fabr. **Adult.** (Plate LXXIV, fig. 3) Body flat and oval, widest towards the posterior end; margins marked by wrinkles forming radial striae; basis capituli wider in front, and as broad as it is long. Hypostome nearly as long as base of capitulum, with four principle rows of teeth. Palps with segments equal, the third the shortest. Spiracles crescentic, transversely elongated and equal in length to the width of the anal ring. Tarsi with a distinct dorsal protuberance. Length 4 to 10 mm.; width 3 to 6 mm. The male *reflexus* is distinguished from the female chiefly by its smaller size.

This species is mainly limited in its distribution to Europe and North Africa; Neumann states that it occurs in California. In France it occurs especially in the Ardennes. It is also common in parts of Germany, Italy, Russia and Roumania. It lives in pigeon coops, hiding in crevices and cracks in the woodwork, and is known in France as the 'pigeon tick'.

Neumann recognizes a variety *magnus* which is larger and narrower than the type; its posterior end is lanceolate in shape. It is found in Equador and California.

Argas persicus, Oken. **Adult.** (Plate LXXIV, figs. 1 and 2) Body flat, oval, and widest towards its posterior end; integumentary folds marked with numerous discs arranged in groups as shown in the figure. The margin is formed of short rectangular festoons, each enclosing a circular pit. Spiracles small and crescentic in shape, equal to about half the width of the anal ring. Basis capituli broader than long; hypostome as long as the base, and armed with four principal rows of teeth. Palps about twice as long as hypostome, second segment the longest. Coxa I in female distinctly separated from coxa II. Tarsi with a dorsal protuberance. The sexes are much alike, but the male is smaller and narrower than the female, its genital orifice is inconspicuous and more posterior in position, and is surrounded by an anal ring. The genital orifice in the female is large and slit-like. Length 4 to 10 mm.; width 2·5 to 6 mm.

Argas persicus can always be distinguished from *reflexus* by its shape, the latter being much narrower anteriorly; the integument is not so finely wrinkled in the former, and coxa I is distinctly separated from coxa II, the other three being contiguous. In *reflexus* all the coxae are contiguous. Neumann recognizes a variety *miniatus* in which the integumentary folds are covered with three to five series of discs, some distance from the margin, and more marked posteriorly; the festoons of the border are as a rule contiguous.

Geographical Distribution: Relation to Disease

This species is found throughout the world, and is always associated with the fowl. In Persia and Egypt it is said to attack man and to inflict a dangerous bite; there is however no definite proof that it carries any disease germ to man. In the case of the fowl it is a serious pest, killing the birds not only by massive infection but by infecting them with *Spirochaetae marchouxi*, Nuttall. This spirochaetosis of fowls was first discovered in Brazil by Marchoux and Salimbene; it is a fatal disease, and in many parts of the world seriously interferes with poultry farming. Spirochaetosis in geese has been recorded from the Trans-Caucasus, and is probably transmitted by *Argas reflexus*.

Argas vespertilionis, Latr. **Male.** (Plate LXXIV, fig. 5.) Flat and broadly oval, with a marked convexity towards the middle third; uniformly brown with a reddish brown margin. Surface marked with fine granulations, and longitudinally radiating discs arranged in about twenty-two lines on the dorsal surface and twenty-eight on the ventral. Anterior end of the body pointed but without any hood. Supracoxal fold moderately marked and extending to a little beyond coxa IV; coxal fold distinct, extending from coxa I to the lower border of coxa IV. Anus situated about the centre of the body, with a well marked transverse fold behind it and extending up towards the coxal fold. Genital opening not conspicuous. All coxae contiguous. Capitulum with a moderately broad base and two distinct hairs on ventral surface at base of hypostome. Female very similar to the male, but readily distinguished from it by the more rounded anterior end and by the large size of the genital opening. Male length 4·2 to 4·8 mm.; width 4·5 to 5 mm. Female, length 5 to 5·5 mm.; width 5 mm.

Bionomics and life history of Argas persicus

The life histories of the ticks of the genus *Argas* are best exemplified by that of *Argas persicus*, which has been carefully studied by Lounsbury. The eggs are laid in cracks and crevices in the woodwork of the fowl coop, or other places where the ticks hide. They are of a shiny brown colour and are laid in batches of from 20 to 100. The larvae (Plate LXXV, fig. 1) hatch out in three weeks or more, according to the temperature; they are ready to feed on about the fourth day after hatching and as a rule attach themselves under the wings, though they may be seen on other parts; they become replete by about the fifth day after attachment. Just prior to leaving the fowl, the body of the larva elongates and flattens, and it is then exactly like a miniature adult. This change appears to be a special adaptation to the environment of the tick, as when it is flat it can more easily pass into narrow cracks, which it at once seeks on dropping from the fowl. It now slowly digests the blood, and after a short interval sheds its skin and the first nymphal instar emerges; it is distinguished from the larva by having eight legs and a pair of spiracles. After a few days it is ready to feed, and this time it only takes from one to two hours to fill itself with blood; it drops off and again crawls into a crevice, where it develops further, emerging after about two weeks as the second nymphal instar. It again goes through the same process and finally, after a period of about two weeks, becomes an adult male or female. The male is smaller and only partially fills itself with blood and may be mistaken for the second nymphal stage; the presence of the genital opening, which is absent in the nymph will, however, suffice to distinguish it. The adults feed about once a month, the female returning after each meal to lay a batch of eggs; during the cold weather the intervals between the feeds are much prolonged. All stages of *persicus*, like most others of the Argatini, can live long periods without food.

The variety *miniatus*, Koch, C. L., which is widely distributed in the United States (Western Texas, Arizona, Florida, Iowa, California), where it is known as the ‘blue bug’, or ‘tampan’, attacks chickens,

Life history of Argas persicus miniatus

pigeons, ducks, geese, turkeys and canaries; it causes serious loss to farmers, either by 'tick worry' (massive infection) or by transmitting spirochaetes. Bishop gives some data regarding its life history in a recent report. The eggs hatch after 10 to 100 days according to the temperature. The larvae attach themselves to their hosts and remain fixed from three and a half to ten days, when they drop off at night and hide in the cracks and crevices in the fowl house. After an interval of from four to seven days the larva moults and the first nymph emerges. The two nymphal stages behave in the same way as those of *persicus*, dropping off immediately they become replete with blood. The female feeds about seven times and is capable of laying as many as 537 eggs; the tick can complete its life history in about forty days.

Life history of Argas vespertilionis

The senior author has studied the complete life history of *Argas vespertilionis*, and has bred a large number from eggs and from larvae. This tick is parasitic on the yellow bat, *Scotophilus kuhli*. The eggs are laid in the resting place of the bat; the larvae hatch in from ten to twelve days, remain attached to the wing of the bat for ten days, and about twenty-four hours before leaving the host become flat like the adult. The following data give the life history of this tick:—

21—10—12	Replete larva dropped during the day.
26—10—12	Changed into first nymph.
30—10—12	Fed to repletion, taking twenty-five minutes to become full.
6—11—12	Changed into second nymph.
10—11—12	Fed to repletion, remaining attached for fifty minutes.
23—11—12	Changed into female; placed with male, when copulation immediately took place, lasting five minutes.
15— 1—13	Fed to repletion, having refused to do so several times before.
21— 1—13	Egg laying began (first batch).
30— 1—13	Egg laying completed.
1— 2—13	First larvae hatched.

GENUS ORNITHODORUS, KOCH, C. L.

Body flat when starving and convex when replete, and may be nearly as broad anteriorly as posteriorly, or pointed and beak-like anteriorly. The margin of the body is not distinct as in the genus Argas, but is of a similar structure to the rest of the integument, which is generally mammilated. On the ventral surface there are two marked folds, one internal *to the coxae, the coxal fold, and the other above the coxae, the supracoxal fold; there is also a transverse pre-anal groove, as well as a transverse post-anal groove. Eyes are either absent, or present in pairs on the supracoxal fold; one pair between coxae I and II, and the other between coxae II and III.* (Neumann)

Neumann gives the following key to the species:—

NEUMANN'S KEY TO THE SPECIES OF ORNITHODORUS

1.	Integument not granular	2
	Integument granular, especially in the anterior part (nymph).	**megnini.** (Mexico; Brazil; United States, Arizona; California; Texas; Iowa.)
2.	Camerostome without lateral flaps or cheeks	3
	Camerostome with lateral flaps	**talaje.** (Brazil; Chili; Mexico; Guatemala; Venezuela; Colombia.)
3.	Last two articles of legs I, II and III with humps on their dorsal borders	4
	Last two articles of legs I, II and III without humps	8
4.	Body nearly as broad anteriorly as posteriorly	5
	Body ending anteriorly in a blunt point	7
5.	Last two articles of legs with separated prominent humps	6
	Last two articles of legs with humps prominent and contiguous.	**pavimentosus.** (S. Africa, Bethany, Namaland.)
6.	With eyes	**savignyi.**
	Without eyes	**moubata.**
7.	With eyes	**coriaceus.** (Mexico; Paraguay.)
	Without eyes	**turicata.** (United States; Mexico; Venezuela.)
8.	Integument not granular, but with fine wrinkles	**lahorensis.** (India, N.-W. Frontier, Lahore.)
	Integument granular	9
9.	Tarsi not forked	10
	Tarsi with marked terminal fork	**furcosus.** (Equador.)
10.	Camerostome prolonged into a cone	11
	Camerostome enlarged in front	**megnini.**
11.	Tarsi provided with three successive dorsal humps	**canestrini.** (Persia; Caucasus.)
	Tarsi with or without one distal dorsal hump	12
12.	Tarsi attenuated at the end	**erraticus.** (Algeria, Tunis.)
	Tarsi with a well marked prominent and pointed dorsal hump.	**tholozani.** (Persia; Caucasus.)

Aragao has recently described a new species of *Ornithodorus*, *O. rostratus*, from the State of Matto Grosso, Brazil, which is not included in the above key; it is characterized as follows: Body round; camerostome visible from the dorsal surface; tarsus I with two dorsal humps, the one situated at the proximal end of the segment pointed and slightly turned towards the extremity of the tarsus. Tarsus IV has only one hump at its distal extremity.

Ornithodorus savignyi, Audoin. **Adult.** (Plate LXXII, figs. 4 and 5.) Body as broad in front as behind. Integument leathery and covered with distinct non-contiguous mammillae, with numerous short hairs interspersed. Supracoxal folds well marked, and with two eyes on each side, the first pair between coxa I and II, and the second between coxa II and III. Coxal folds less marked. Pre-anal groove distinct. Basis capituli broader than long and shorter than the rest of the rostrum; hypostome with six principle rows of teeth, the external the stoutest. Palps with first and second segments of equal length; third segment the shortest. Coxae contiguous; protarsus and tarsus of legs I, II and III with three well marked humps; the two proximal humps on tarsus of leg IV are close to each other, while the third is separated by an interval equal to about two and a half times the distance between the first and second. Length 5 to 12 mm., width 4 to 8·5 mm. The male and female resemble each other, except that the former is smaller, its genital orifice being markedly smaller. In the female it is a broad transverse slit which can be made to gape, and is guarded by two flap-like valves; in the male the orifice is oval and the valves are absent.

Geographical distribution

This species is widely distributed, and is found in Arabia, Nubia, Egypt, Somaliland, Abyssinia, German East Africa, Cape Colony, Rhodesia, Bechuanaland, and Portuguese East Africa. In India it is common in the Madras Presidency, in Gujarat and in many parts of the Bombay Presidency. In Aden it is widely distributed throughout the Hinterland, where its principle host is the camel.

Bionomics: Relation to Disease

This tick often attacks man, and the senior author has seen extensive ecchymosis following its bite, but never any constitutional symptoms. Its bite is popularly believed to be the cause of the Aden Sore, but there is no evidence to support this belief. Throughout the Aden Hinterland and in Somaliland *savignyi* is abundant along all the camel caravan tracks, and all the resting places literally swarm with the immature stages. The adults are commonly seen attached around the anus of the camel. In South India it is common in the sand under large trees, particularly in those places where cattle rest; the blood of these animals appears to be its

PLATE. LXXV.

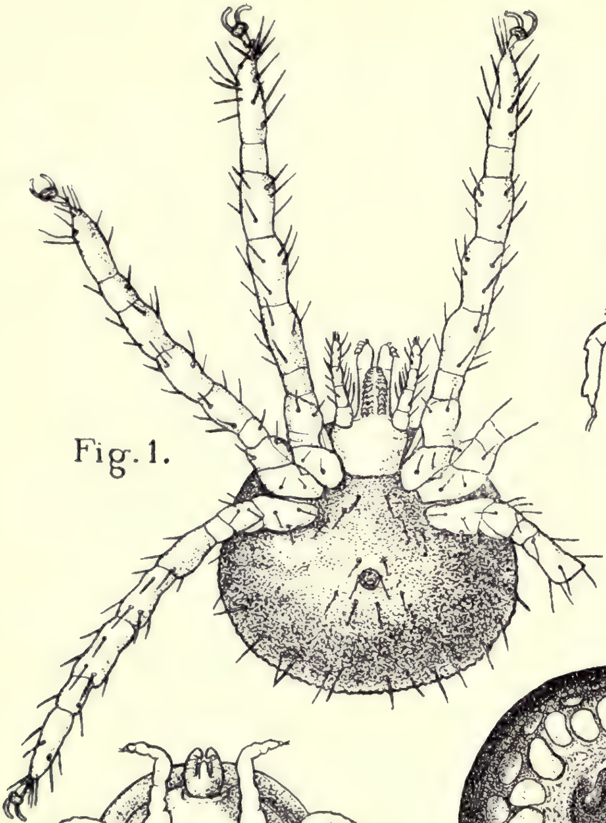


Fig. 1.

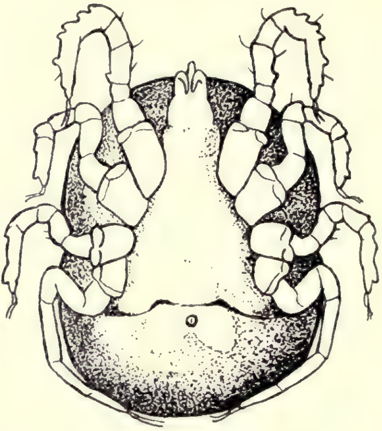


Fig. 2.

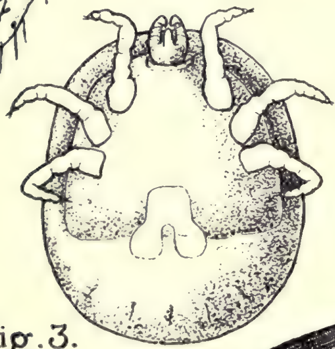


Fig. 3.

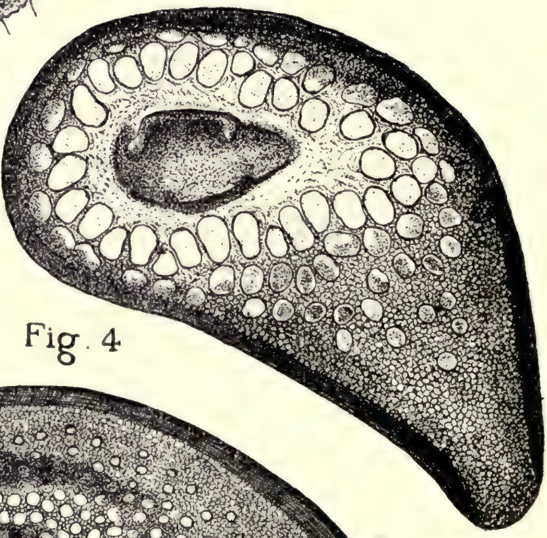


Fig. 4

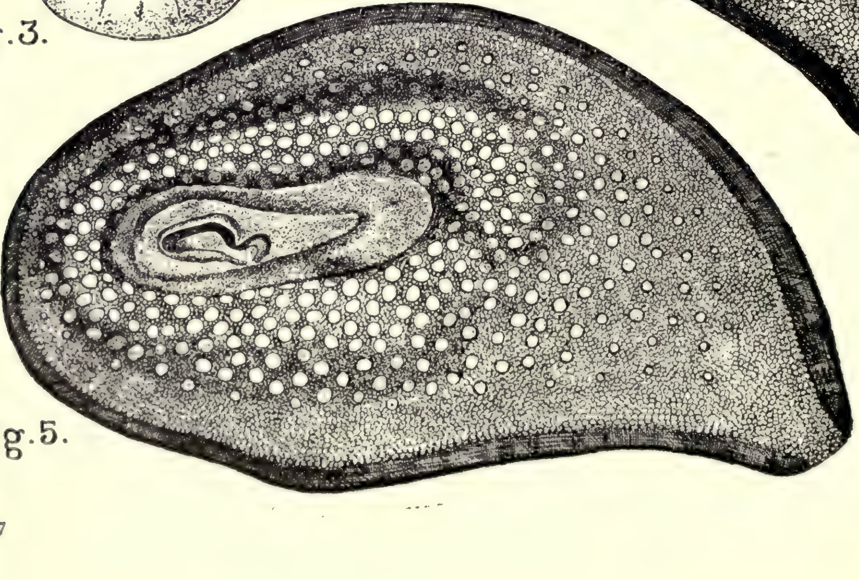


Fig. 5.

PLATE LXXV

Figure 1. Larva of *Argas persicus.* × 40.

Figure 2. First nymph of *Ornithodorus savignyi.* × 24.

Figure 3. Larva of same. × 30.

Figure 4. Stigmal plate of *Dermacentor venustus,* ♂. Note the broad aperture, prominent terminal prolongation and the scattered pores; greatly enlarged, after Stiles. *Dermacentor venustus,* Marx, as interpreted by Stiles includes *venustus,* Marx, and *andersoni,* Stiles.

Figure 5. Stigmal plate *Dermacentor reticulatus,* ♂ (France). Note the elongate form of the plate; the aperture is also elongate and situated more towards the interior end (head). The pores are numerous and thickly set around the aperture; greatly enlarged, after Stiles.

main food. It is also common in some of the third class waiting sheds on the South Indian Railway. In South India it is said to cause a particular kind of fever, but there is no reliable information on this point. It can have nothing to do with the spread of Kala Azar, for the parasite fails to flagellate in its alimentary tract, and it has never been seen in any of the houses in the endemic areas in Georgetown in Madras. Drake-Brockman, who recently reported the occurrence of an outbreak of relapsing fever at Bulhar in Somaliland, states that he failed to find a single specimen of *Ornithodorus moubata*, the species which transmits the spirochaete of this disease in British East Africa; *savignyi* was abundant in all the native huts and was probably acting as the carrier.

Life history of Ornithodorus savignyi

The *egg* of *savignyi* measures from 1·3 to 1·5 mm. in length and from ·8 to 1 mm. in width. It is ovoid in shape and of a dark brown to black colour with a smooth shiny surface. The eggs are laid in batches of from 50 to 100 or more, and hatch in about fourteen days. The larva (Plate LXXV, fig. 3) is sub-circular in shape, and of the same colour as the egg; it measures 1·75 mm. in length and about 1 mm. in width. On hatching it frees itself from the egg shell, and remains in a dormant condition for about ten days, when it moults and the first nymphal instar emerges; it never sucks blood. The first nymphal stage (Plate LXXV, fig. 2) is of a light brown colour, and measures from 1·75 to 2 mm. in length and from 1·5 to 1·8 mm. in breadth; it resembles the adult, having eight legs, and it is extremely active. About two to three days after emerging from the larval state it will feed, taking from fifteen to thirty minutes to become replete with blood. It then drops off, and under natural conditions buries itself in the sand; the following data give the time occupied by the several stages of this tick.

9—9—11	First nymphal instar emerged.
12—9—11	First feed.
16—9—11	Second feed.
21—9—11	Second nymphal instar emerged.
25—9—11	First feed.
2—10—11	Third nymph emerged.
10—10—11	First feed.
14—10—11	Second feed.
16—10—11	Fourth nymph emerged.
28—10—11	First feed.
31—10—11	Second feed.
7—11—11	Adult emerged.

From the above it will be noted that *O. savignyi* has four nymphal stages; the period from the egg to the adult is about eighty-four days, and during this time it feeds at least seven times.

A female and two males, which had emerged on 30-10-1911, were kept together in the same petri dish; the following data give the number of feeds and eggs laid.

10—11—11	Female fed for the first time.
15—11—11	Second feed.
28—11—11	Egg laying began; when completed 106 eggs were collected.
2—12—11	Third feed.
4—12—11	Began laying second batch of eggs; when completed eighty-one eggs were collected.
5— 1—12	Fourth feed.
19— 1—12	Fifth feed.
28— 1—12	Began laying third batch of eggs; eighty eggs were collected later.
1— 3—12	Sixth feed.
8— 3—12	Began laying fourth batch of eggs; 250 were collected later.
27— 4—12	Seventh feed.
16— 5—12	Began laying fifth batch of eggs; 200 eggs were collected later.
26— 6—12	Eighth feed.
31—10—12	Ninth feed.
10—11—12	Began laying sixth batch of eggs; 195 eggs collected later.
26—12—12	Female died without laying any more eggs.

The two males died on 1-3-12 and 10-4-12 respectively; they fed in all four times. The above observations will give some idea of the length of life and egg laying capacity of this tick.

Ornithodorus moubata, Murray. **Adult** (Plate LXXIV, fig. 6). Body almost as broad anteriorly as posteriorly, covered with non-contiguous mammillae, but with fewer hairs than *savignyi*. Basis capituli broader than long and shorter than the palps; hypostome with six principle rows of teeth. Tarsi of legs I, II and III with three humps as in *savignyi*; those on the protarsus are sub-equal, more pointed and about equidistant, while those of *savignyi* are unequal, less pointed and not equidistant. The tarsus of leg IV of *moubata* is shorter and thicker than that of *savignyi*, and its humps are nearly equidistant. Eyes absent. Length 8 to 12 mm.; breadth 6 to 10 mm.

Ornithodorus moubata is found in the following regions of Africa:—From British East Africa to the Transvaal, and across to the Congo; southward to German East Africa and Cape Colony. It is common in Egypt, Abyssinia, in parts of Somaliland, and in Portuguese East Africa. *Moubata* is essentially a human parasite, and is found in huts and houses, principally those of natives. It hides in cracks in the mud walls, in mats and in the dust of the floors and bed platforms; it crawls out, like the bed bug, to bite at night. Its habit of hiding in mats explains how it may be carried about by the natives from place to place.

Geographical Distribution: Bionomics

As is well known, *moubata* is the invertebrate host of *Spirochaeta duttoni*, the parasite of African Relapsing Fever. This spirochaete, on being taken into the alimentary tract of the female, penetrates her ova, thus infecting the larvae. The first nymph transmits the spirochaete when it sucks blood, though the exact route by which the parasite reaches the vertebrate host is not definitely decided (see Chapter XII). All the succeeding instars are also infective; a tick once infected may remain infective for an indefinite period. It is also known that the spirochaete may pass to the third generation, though the intermediate stages are fed on uninfected blood. It is very doubtful whether the so-called spirochaete granules from the Malpighian tubes of *moubata* represent a stage in the life history of the parasite; similar granules have been found in other species of ticks which have never been infected with spirochaetes.

Relation to Disease

The *egg* of *moubata* is ovoid in shape, of a glistening dark yellowish colour, and measures ·9 by ·8 mm. The larva hatches out in from eight to thirteen days, and remains in its egg case until the first nymphal instar emerges. Like *savignyi*, *moubata* has four nymphal stages.

Mr. Howlett informs one of the writers that *Ornithodorus lahorensis* is a well known human pest in many parts of Baluchistan; it is, however, usually found on sheep. It is possible that some of the undifferentiated fevers of the North-West Frontier of India may be associated with its presence.

SECTION IXODINI

Ticks with a dorsal shield and a terminal capitulum; the second and third segments of the palps are scooped out, especially in the female; the fourth segment consists of a small papilla of a tactile nature situated in a depression on the infero-lateral surface of the third segment. The spiracles are situated behind coxa IV. Tarsi armed with hooks and a pulvillum. Sexual dimorphism well marked, the scutum of the male covering the whole of the dorsum, leaving only a narrow border usually divided posteriorly into eleven quadrangular festoons; in the female the scutum consists *of a small shield situated behind the capitulum. Porose areas present on the dorsum of the capitulum of females; eyes if present situated at sides of anterior end of scutum.* (Neumann)

Neumann divides the Ixodini into three tribes as follows :—

Male with several non-salient ventral shields . .	Tribe **Ixodaria.**
Male with two adanal shields	Tribe **Rhipicephalaria.**
Male without ventral shields or plates, but with plaques (Dönitz)	Tribe **Amblyommataria.**

TRIBE IXODARIA

Anal groove surrounds anus anteriorly; it may be open or closed posteriorly and is not connected with the genital groove. Capitulum elongated. Eyes absent. Posterior festoons wanting. Spiracle circular or oval. Male with ventral shields as follows:—one anterior to the genital orifice, the pregenital, a second, the median, between the genital and anal openings, a third, the anal, on which the anus is situated; an epimeral plate lying laterally, on which the coxae and spiracles are situated; one adanal plate situated at each side of the anal. (Neumann)

The ticks belonging to this tribe are very characteristic; they are all of a brown colour, and their dorsal shields are without any ornamentation. Except for one species, *Ceratixodes putus*, Cambridge, their tarsi are without spurs. The second palpal segment is nearly always narrowed, thus leaving a space between it and the hypostome; this character gives the ticks a striking appearance.

Neumann divides the Ixodaria into one genus *Ixodes*, and three subgenera *Ixodes*, *Ceratixodes* and *Eschatocephalus*. The characters of the genus *Ixodes* are those of the tribe Ixodaria ; he gives the following key to the subgenera.

NEUMANN'S KEY TO THE SUBGENERA OF IXODES

1.	Palps hollowed out on their internal surfaces in both sexes .	**Ixodes.**
	Palps convex on their internal surfaces in the male	2
2.	Third article of the palps of the male terminating in a point at its distal extremity	**Ceratixodes.**
	Third article of the palps of the male thickened at its extremity	**Eschatocephalus.**

SUB-GENUS IXODES (LATR.), NEUMANN

Second and third segments of the palps in both sexes hollowed out on their internal surfaces; the palps are shorter in the male than in the female. Tarsi without terminal spurs. (Neumann)

Neumann gives the following key to the identification of the species:—

NEUMANN'S KEY TO THE SPECIES OF IXODES

MALES

1.	Palps hollowed out on their internal surfaces	**2**
	Palps convex on their internal surfaces	**14**
2.	Anal grooves parallel or divergent	**3**
	Anal grooves convergent	**11**
3.	Scutum covering almost the whole of the dorsum	**4**
	Scutum covering the middle half of the dorsum	**loricatus.** (Brazil; Argentine; Paraguay.)
4.	Coxa I spurred	**5**
	Coxa I without spurs	**10**
5.	Tarsi without dorsal humps	**6**
	Tarsi with sub-terminal dorsal hump	**9**
6.	Coxa I either without external spur or with an external one shorter than the internal	**7**
	Coxa I with two short equal spurs	**coxaefurcatus.** (Egypt.)
7.	Coxa I has a very long internal spur	**8**
	Coxa I has a short internal spur, double the length of external.	**minor.** (Guatemala.)
8.	Coxa I without external spur	**ricinus.** (Europe; United States; Caucasus; Asia Minor; Japan; China; Algeria.)
	Coxa I has a well developed external spur	**boliviensis.** (Bolivia.)
9.	Coxa I has a very long internal spur	**cookei.** (United States, Texas, Massachusetts.)
	Coxa I has a short internal spur	**hexagonus.** (England; France; United States.)
10.	Anal plate has parallel sides	**rubicundus.** (Cape Colony; Congo.)
	Anal plate broader posteriorly than anteriorly	**tenuirostris.** (Great Britain; Germany.)
11.	Anal plate open posteriorly	**12**
	Anal plate circular	**rasus.** (Africa, Congo, Togo Land, Cameroons.)
12.	Anal plate in the shape of a horse-shoe	**pilosus.** (S. Africa.)
	Anal plate terminating in a point posteriorly	**13**
13.	Anal plate sub-circular (racket-shaped)	**ugandanus.** (Uganda.)
	Anal plate sub-rectangular	**holocyclus.** (Australia.)
14.	Third segment of palp terminating in a point, legs of medium length (*Ceratixodes*)	**putus.**
	Third segment of palp thickened at summit, legs very long (*Eschatocephalus*)	**vespertilionis.**

FEMALES *

1.	Anal groove prolonged behind the anus	2
	Anal groove forming a circle round the anus	**rasus**.
2.	Anal groove with parallel or divergent arms	3
	Anal groove with markedly convergent arms	41
3.	Coxa I with internal spur	4
	Coxa I without internal spur	29
4.	Coxa I with a very long internal spur	5
	Coxa I with a short internal spur	19
5.	Basis capituli with hump on ventral surface below each palp	6
	Basis capituli without ventral hump	15
6.	Coxa I without external spur	7
	Coxa I with external spur	9
7.	Scutum with lateral grooves	8
	Scutum without lateral grooves	**spinicoxalis**. (Sumatra.)
8.	Porose areas large, somewhat near each other	**ricinus**.
	Porose areas small, widely separated	**dentatus**. (United States.)
9.	Second article of palps much longer than the third	10
	Second and third articles of palps sub-equal	13
10.	Tarsi tapering, without dorsal protuberance	11
	Tarsi with dorsal protuberance near the extremity	**fossulatus**.
11.	Ventral hump on basis capituli reduced to a tuberosity	**affinis**. (Costa Rico ; United States.)
	Ventral hump on basis capituli longer than broad	12
12.	External spur of coxa I as broad as it is long, hypostome with six rows of teeth	**fuscipes**. (Brazil.)
	External spur of coxa I longer than broad, hypostome with eight rows of teeth	**bicornis**. (Mexico.)
13.	First segment of palp prolonged ventrally to a point	**diversifossus.** (New Mexico.)
	First segment of palp not prolonged	14
14.	Scutum longer (1·3 mm.) than broad (1·25 mm.)	**boliviensis**.
	Scutum much longer (1·4 mm.) than broad (0·9 mm.)	**acuminatus**.
15.	Tarsi without dorsal hump near the extremity	16
	Tarsi with dorsal hump near the extremity	**cookei**
16.	Coxa I with external spur much shorter than the internal	17
	Coxa I with external spur nearly as long as the internal	**acutitarsus**. (India ; Japan ; Formosa.)
17.	Scutum oval	18
	Scutum sub-circular	**sculptus**. (California.)
18.	Scutum with very fine punctations, tarsi long and thin	**nigricans.** (Madeira.)
	Scutum with large punctations, tarsi short and humped	**rubidus.** (Mexico.)

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* When the distribution is given for the male, it is not repeated for the female ; in the case of species described in the text the distribution is given there.

19. Tarsi with dorsal hump near the extremity . . . . . **hexagonus.**

Tarsi without dorsal hump 20

20. Scutum as broad or broader than long 21

Scutum longer than broad 22

21. Scutum without lateral grooves, porose areas small, set widely apart . . . . **luteus.** (Africa.)

Scutum with lateral grooves, porose areas large, oval and near each other . . . . **ovatus.** (Japan.)

22. Base of capitulum with ventral hump behind each palp 23

Base of capitulum without ventral hump 28

23. First segment of palp cylindrical without projections 24

First segment of palp angular, forming a projection directed forwards . . . . **auritulus.** (Tierra del Fuego.)

24. Coxa I with large flat spurs of equal size . . . . . **loricatus.** (Brazil ; Argentine ; Paraguay ; Tierra del Fuego.)

Coxa I with unequal spurs 25

25. Scutum a little longer than broad 26

Scutum nearly twice as long as broad with numerous punctations. . . . **minor.**

26. Scutum with cervical grooves and distinct punctations 27

Scutum without cervical grooves, punctations few and indistinct . . . . **nitens.** (Christmas Island.)

27. Scutum lozenge-shaped, broadest in middle . . . . . **frontalis.** (France ; Italy ; England ; Germany ; United States.)

Scutum pyriform, broadest anteriorly . . . . . . **brunneus.** (North America, Texas.)

28. Porose areas large and sub-triangular, near each other . . **angustus** (Canada ; United States ; Argentine.)

Porose areas small, circular, and widely separated . . . **granulatus.** (Burma ; Java.)

29. Coxa I with external spur 30

Coxa I without spur 32

30. Tarsi attenuated and indented . . . . **eudyptidis.** (New Zealand ; Japan.)

Tarsi gradually attenuated 31

31. Porose areas large and close together . . . . . . **percavatus.** (Nightingale Island.)

Porose areas fused together . . . . **unicavatus.**

32. Tarsi with dorsal protuberance near the extremity 33

Tarsi without dorsal protuberance 35

33. Scutum longer than broad 34

Scutum broader than long, sub-circular . . . . . . **vestitus.** (Australia.)

34. Scutum lozenge-shaped, palps markedly hollowed out internally . . . . **hexagonus,** sub-species **inchoatus.** (France ; England.)

	Scutum sub-triangular, palps slightly hollowed out internally (*Ceratixodes*)	**putus**.
35.	First segment of palp narrow, not ensheathing hypostome	**36**
	First segment of palp broadened and ensheathing hypostome	**tasmani**. (Australia ; Tasmania.)
36.	First segment of palp not prolonged	**37**
	First segment of palp prolonged ventrally or laterally	**40**
37.	Scutum as broad as long, sub-circular, basis capituli without horns	**japonensis**. (Japan, Tokio.)
	Scutum longer than broad	**38**
38.	Scutum a little longer than broad, legs of medium length	**39**
	Scutum very much longer than broad, legs very long (*Eschatocephalus*)	**vespertilionis**
39.	Basis capituli with ventral hump behind each palp	**rubicundus**.
	Basis capituli without ventral humps	**simplex**. (Shanghai ; French Congo, Gaboon.)
40.	First segment of palp in the form of a transverse spur longer than broad	**tenuirostris**.
	First segment of palp with a hump on ventral surface, scutum much broader than long	**ornithorhynchi**. (Tasmania.)
41.	Anal groove open posteriorly	**42**
	Anal groove pointed posteriorly	**45**
42.	Basis capituli with ventral hump behind palp	**43**
	Basis capituli without ventral hump, anal groove prolonged behind in the form of a racket	**ugandanus**.
43.	Scutum as broad as long with superficial punctations and lateral groove, coxa I with a very short internal spurs	**pilosus**.
	Scutum much longer than broad ; coxa I with a very well developed internal spur	**44**
44.	Coxa I with nearly obsolete external spur, scutum with large punctations	**schillingsi**. (Mozambique.)
	Coxa I with long external spur, scutum with fine punctations	**lunatus**. (Madagascar.)
45.	Palps long, first segment not thick	**holocyclus**.
	Palps short, first segment dilated, ensheathing the base of the hypostome	**australensis**. (Australia.)

Ticks of the genus *Ixodes* are widely distributed, and have been recorded from Europe, Africa, Asia, Australia and North and South America, the latter continent being specially rich in species. Only one species, *Ixodes acutitarus* has been recorded from India (Darjeeling) ; not a single species has been found in South India.

Ixodes ricinus, L. **Male**. (Plate LXXVI, fig. 1.) Anal groove with arms slightly divergent posteriorly. Coxa I with a well developed spur overlapping coxa II. Tarsi long and slender, without dorsal humps.

PLATE CCXVI.

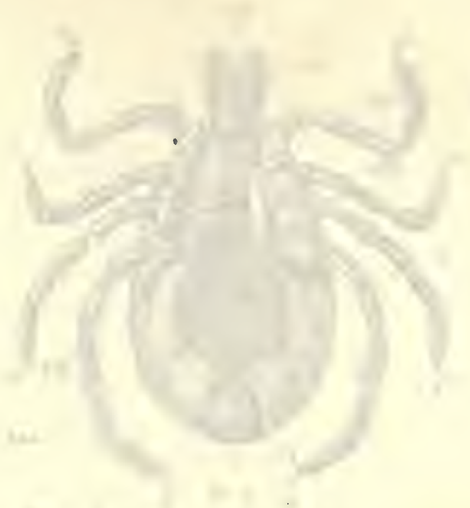
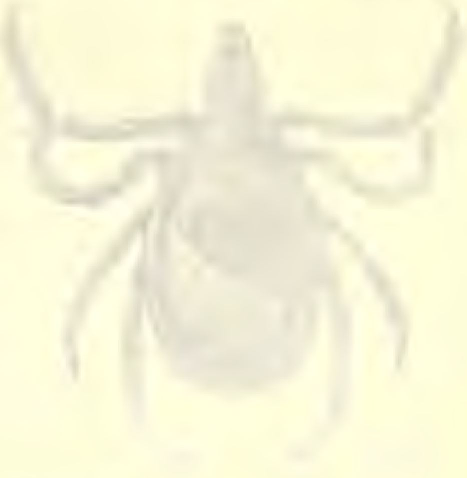


Fig. 1.



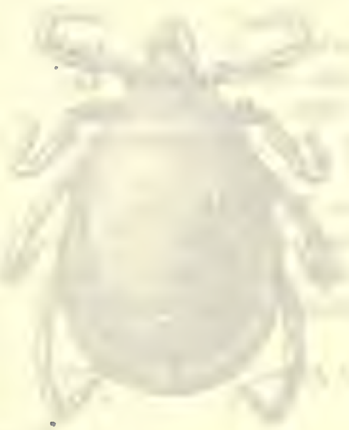
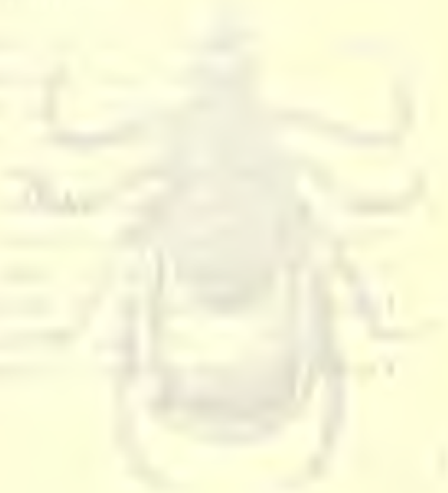


Fig. 3.



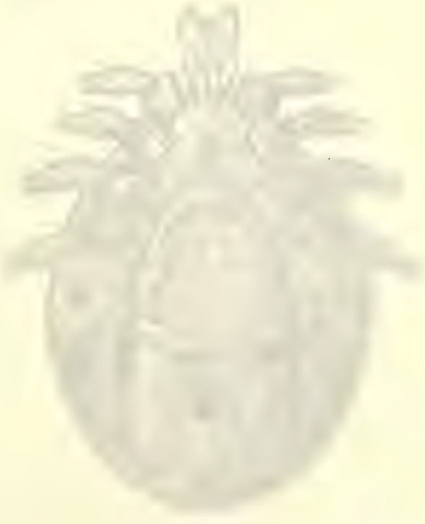


Fig. 5.

Fig. 6.

PLATE LXXVI

Figure 1. Ventral view of *Ixodes ricinus*, ♂. a.g., anal groove. an.p., anal plate. epp., epimeral plate. gg., genital groove. gp., genital plate. Hy., hypostome. m.p., median plate. p., palp. pgp., pre-genital plate. sp., spiracle. × 22.

Figure 2. Dorsal view of *Ixodes ricinus*, ♀. × 18.

Figure 3. Dorsal view of *Ixodes angustus*, ♂. × 22.

Figure 4. Dorsal view of *Ixodes angustus*, ♀. × 20.

Figure 5. Ventral view of *Eschatocephalus vespertilionis*, ♂. × 18, after Neumann.

Figure 6. Ventral view of *Ceratixodes putus*, ♂. × 17, after Neumann.

PLATE. LXXVI.

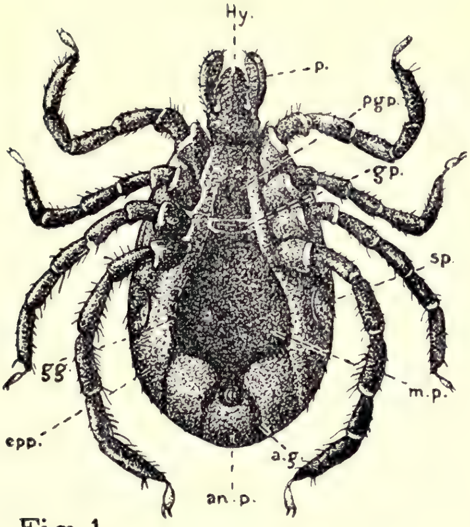

Hy.
p.
pgp.
gp.
sp.
gg.
m.p.
epp.
a.g.
an.p.

Fig. 1.

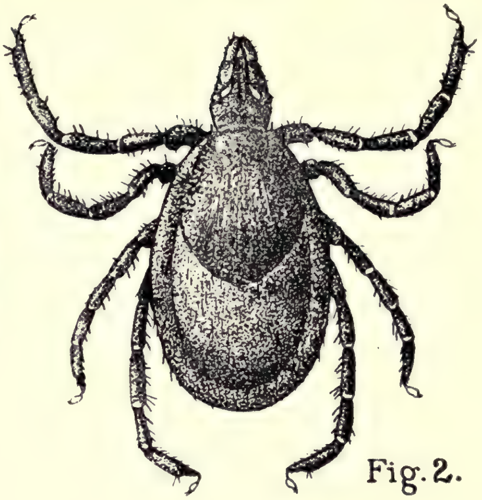


Fig. 2.

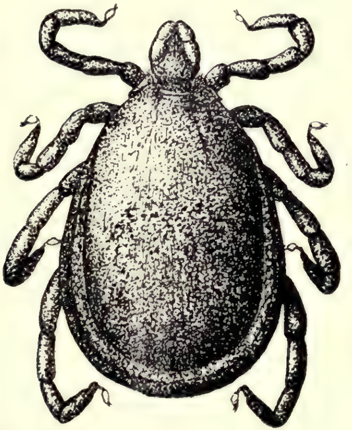


Fig. 3.

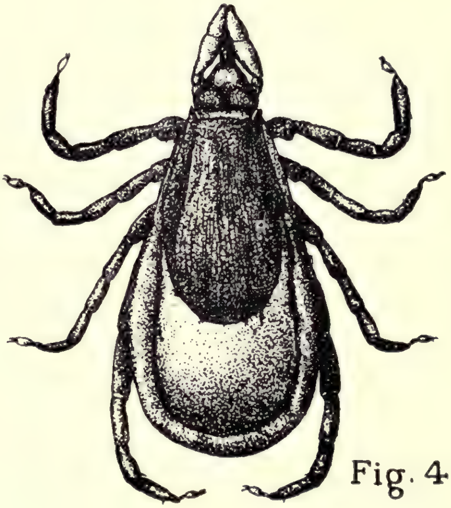


Fig. 4.

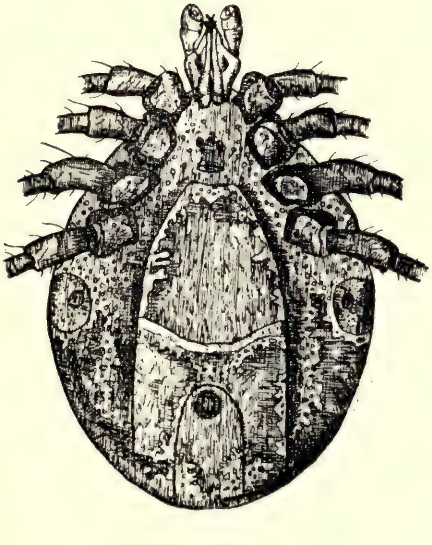


Fig. 5.

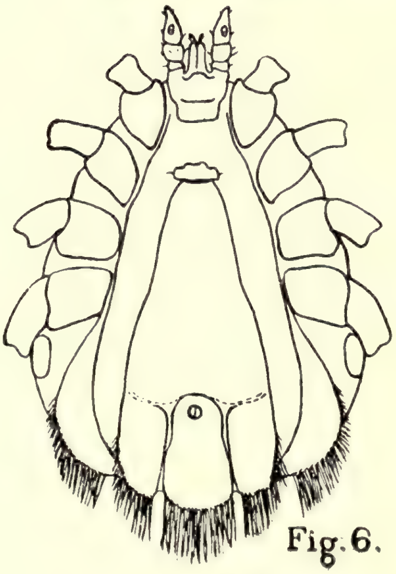


Fig. 6.

First article of palp not prolonged. Scutum pubescent with numerous fine punctations. Pre-genital plate one-third longer than broad. Hypostome with six to eight rows of marginal teeth united by crenulations. Length 2·5 mm.; width 1·5 mm. (Neumann)

Female. (fig. 2.) Scutum longer than broad; cervical grooves superficial; lateral grooves short. Basis capituli with slight hump behind each palp. Porose areas large and pyriform in shape. Hypostome lanceolate, with six rows of teeth. Length 3·5 to 10 mm.; width 3·75 to 7 mm. (Neumann)

This species is found throughout Europe; it also occurs in Asia Minor, Japan, China, Caucasus, Algeria, Madeira and the United States. It has been found on a large number of different animals and on man. In Europe it is said to transmit *Piroplasma bigeminum.*

Ixodes angustus, Neumann. **Male.** (Plate LXXVI, fig. 3.) Anal groove with slightly divergent posterior arms. Coxa I bidentate, internal spur well developed, external small; there are small spurs on the remaining coxae. Tarsi moderately long; tarus IV tapering obliquely. First segment of palp not prolonged. Scutum convex with many fine punctations. Hypostome small with three rows of sub-equal teeth.

Female. (fig. 4.) Anal groove with slightly divergent posterior arms. Coxa I with two short flat spurs, remaining coxae with similar external spurs. Tarsi long and tapering, and without dorsal humps. First segment of palp not prolonged. Basis capituli smooth on ventral surface; porose areas large and sub-triangular. Scutum longer than broad, sub-oval. Cervical grooves superficial, lateral grooves marked with numerous unequal punctations. Hypostome straight, with four rows of teeth.

Ixodes angustus is found in the United States, Canada and the Argentine Republic; it is common on the squirrel, *Sciurus hudsonius douglasi.*

SUB-GENUS CERATIXODES, NEUMANN.

Palps convex on their internal surfaces, third segment conical in the male; the fourth in the male is inserted near the proximal end of the third, while in the female it is inserted near the distal extremity. (Neumann)

Ceratixodes putus, Cambridge. **Male.** (Plate LXXVI, fig. 6.) Anal groove with parallel arms; coxae without spurs. First segment of palp not prolonged. Scutum glabrous with straight marginal fold; cervical grooves long and rather deep, punctations numerous. Posterior marginal fold divided into five festoons, bordered with long hairs, the external ones gradually shortening. Pre-genital plate wanting; genito-anal plate triangular; anal and adanal plates sub-rectangular and twice as long as broad. Hypostome short, bifid, with rudimentary teeth. Palps long and conical, concave on the dorsum, the fourth segment perpendicular to the third and inserted at or near its base. Tarsi tapering, provided with two small contiguous and terminal spurs. Length 4 mm.; width 2·5. mm. (Neumann)

Female. Scutum longer than broad, sub-triangular, cervical grooves convergent anteriorly; lateral grooves absent; numerous fine punctations; palps broad, hollowed out internally, third segment broad, the fourth terminal. Hypostome long, not bifid, borders parallel, with four rows of sharp marginal teeth. Tarsi with dorsal protuberance. Length 4 to 10 mm.; width 3 to 7 mm. (Neumann)

This species is widely distributed, occurring in Alaska, Behring Island, King Island, Tasmania, Cape Horn, Campbell Island. New Zealand, Kerguelen Island, Indian Ocean, Falkland Island; also in certain parts of England, Scotland and Wales. It is a parasite of marine birds and infests their breeding places.

SUB-GENUS ESCHATOCEPHALUS, FRAUENFELD

Palps pyriform and thickened at the distal extremity in the males; valvular in the female.

Eschatocephalus vespertilionis, Koch, C. L. **Male.** (Plate LXXVI, fig. 5.) Anal groove with long parallel arms. Coxae without spurs. Legs very long, tarsi long, attenuated. First segment of palp not prolonged. Scutum not well defined and divided into three longitudinal zones with coarse punctations. Ventral plates as follows;—pre-genital small; genito-anal short and broad; anal plate ogival, twice as long as broad; adanal long and straight. Capitulum short; hypostome lanceolate, sloping at the distal extremity, membraneous; teeth rudimentary. Length 4 mm.; width 2·7 mm. (Neumann)

Female. Scutum much longer than broad, oval; cervical groove superficial; punctations fine. Porose areas large, sub-triangular and broader than long. Palps long, and flat; hypostome pointed and lanceolate with six to eight rows of teeth. Length 4 to 8 mm.; width 2 to 6 mm. (Neumann)

This tick has up to the present only been found on bats, in many parts of the world.

Ticks belonging to the genus *Ixodes* require three different animals to feed on in their larval, nymphal and adult stages. Lounsbury has carefully studied the life history of *Ixodes pilosus*, the so-called 'paralysis tick' of South Africa. This tick is essentially a parasite of warm-blooded animals, and appears to thrive best on the ox, sheep and goat, though it has been found on many other animals and even on man. It prefers to attach itself to the head, and especially to the ears, but may be found on any part of the body. The larval *pilosus* takes about two or three days to become replete with blood; this time may, however, be greatly lengthened. It then drops off and seeks a hiding place, where it slowly digests its food and later becomes transformed into the nymph. It again seeks a host, to which it remains attached for three days; it then drops off and slowly becomes transformed into the adult. If both sexes become attached to the third host at the same time copulation take place, and the female becomes replete with blood in from five to six days. This type of life history is common to the majority of the Ixodidae and is a relatively simple one; it should, however, be clearly understood that it does not necessarily follow that the nymph will attach itself to the same species of animal as that on which the larvae fed, and the adult to the same species on which the nymph fed; each stage may feed on a different species of mammal or reptile.

Life history of ticks of the genus Ixodes.

TRIBE RHIPICEPHALARIA

Anal groove (sometimes absent) contouring the anus posteriorly, arms extending anteriorly and joining the genital grooves at the level of the spiracles. Palps hollowed out internally; eyes present. Usually eleven festoons along the posterior border. Scutum sometimes marked with clear spots. Ventral surface of male with four plates or shields; a quadrangular adanal plate at each side of the anus and an accessory triangular one, which is smaller and situated external to the adanal. (Neumann)

Neumann gives the following key to the genera :—

NEUMANN'S KEY TO THE GENERA OF RHIPICEPHALARIA

Capitulum short, basis capituli with lateral projections; spiracles sub-triangular. Anal grove present	**Rhipicephalus.**
Capitulum short, basis capituli with lateral projections; spiracles circular or oval. Anal groove absent . . .	**Margaropus.**
Capitulum long, basis capituli without projections, lateral borders straight and parallel; spiracles sub-triangular. Anal groove present	**Hyalomma.**

GENUS RHIPICEPHALUS, KOCH, C. L.

Capitulum short, basis capituli hexagonal, with lateral projections on the dorsal aspect on each side. Palps short, broad and flat on the dorsal surface, the external border straight or convex. First segment of palp prolonged internally on the ventral surface and bearing a number of feathery hairs; the same border of the second and third segments also with hairs. Hypostome with six rows of teeth. Spiracles comma-shaped, long in the male and short in the female. Coxa I bidentate, the internal spur broad and flat, the external conical; the remaining coxae with very short external spurs; tarsi with one or more spurs. Anal groove present. Posterior festoons well marked in the male and in the unfed female. Scutum usually inornate but sometimes marked with clear spots. Eyes situated at the sides of the scutum, about half way down in the female. (Neumann)

The genus *Rhipicephalus* is essentially African; a few species, however, are found in Southern Europe and some in Asia. It is represented in America by one species, *R. sanguineus*, and not at all in Australia.

Neumann gives the following key for the determination of the species:—

NEUMANN'S KEY TO THE SPECIES OF RHIPICEPHALUS

MALES

1.	Eyes flat	
	Eyes hemispherical	22
2.	Marginal groove present	3
	Marginal groove absent	17
3.	Scutum unicoloured, brown	4
	Scutum white and black	**pulchellus**.
	(Zanzibar; Somaliland; Massailand; Abyssinia; German East Africa.)	
4.	Adanal plates not prolonged into points (posterior borders straight or convex)	5
	Adanal plates prolonged into one or two points (posterior borders concave)	15
5.	Posterior border smooth or with a caudal appendage	6
	Posterior border with a caudal appendage	**aurantiacus**. (Liberia.)
6	Adanal plates triangular or sub-triangular (internal borders straight or slightly concave)	7
	Adanal plates sickle-shaped (internal border very concave, posterior and external borders forming a regular curve)	**haemaphysaloides**. (China; Sumatra; Java; Borneo; Burma; India; Ceylon.)
7.	Coxa IV with very short spurs, much shorter than the coxa	8
	Coxa IV with long spurs, the external much longer than the coxa	**gladiger**. (Congo.)

8. Marginal grooves long and deep, commencing near the eyes 9

Marginal grooves superficial, short, and commencing at about half the length of the body . . . . **ziemanni**.
(Cameroons; Liberia.)

9. Scutum with sparsely scattered punctations absent in places 10

Scutum with numerous and closely set punctations 13

10. Scutum with unequal punctations, clearly marked and distributed irregularly 11

Scutum with large equal punctations, usually in longitudinal rows, intermixed with fine indistinct punctations . . . **simus**.

11. Coxa I either with no anterior projection, or only a short one, not visible on the dorsal surface 12

Coxa I with a long anterior projection visible on the dorsal surface . . . . **appendiculatus**.

12. Scutum with coarse and fine punctations regularly distributed. **sanguineus**.

Scutum with medium-sized punctations equally distributed between the lateral grooves, sparse in their neighbourhood, absent on the border; some large ones in scapular angle . **longus**.
(Congo; Kasongo.)

13. Scutum with punctations distributed throughout the whole surface 14

Scutum with no punctations on either side in the depression between the cervical and marginal grooves . . . . **supertritus**.
(Congo; Nyasaland.)

14. Scutum with markedly unequal punctations, mostly fine and non-contiguous . . . . **bursa**.

Scutum with large sub-equal deep contiguous punctations, in lines often separated by ridges . . . . **capensis**.

15. Adanal plates pointed internally 16

Adanal plates with an external point . . . . **tricuspis**.
(Congo; Transvaal.)

16. Coxa I without a projection visible from the dorsum, adanal plates with two points . . . . **armatus**.
(Somaliland.)

Coxa I with a projection visible on the dorsum, adanal plates with one point . . . . **duttoni**.
(Congo, Zambu.)

17. Scutum with numerous white spots . . . . **maculatus**.
(Cameroons.)

Scutum without spots, or with one diffuse spot in the centre 18

18. Adanal shields triangular, without a point on the posterior hump 19

Adanal shields quadrangular, with an internal point on the posterior hump . . . . **cuspidatus**.
(Senegal.)

19. Coxa I half the size of the adanal plate 20

Coxa I as long as the adanal plate . . . . **longicoxatus**.
(German East Africa.)

20. Basis capituli as long as broad, with slightly projecting lateral angles . . . . **ecinctus**.
(British East Africa.)

Basis capituli broader than long with projecting lateral angles. 21

21. Median festoon without caudal appendage . . . . . **kochi.**
(Zanzibar.)

One or three caudal appendages . . . . **auriantiacus.**
(Liberia.)

22. Scutum reddish brown with scattered punctations, legs reddish brown . . . . **oculatus.**
(British and German East Africa.)

Scutum a dull dark brown (punctations close, legs reddish yellow) . . . . **evertsi.**

FEMALES

1. Eyes flat 2

Eyes hemispherical 20

2. Scutum brown 3

Scutum white 19

3. Coxa IV with very short spurs, usually much shorter than the coxa 4

Coxa IV with long spurs, the external much longer than the coxa . . . . **gladiger.**

4. Scutum elongated, longer than broad 5

Scutum short oval, or as broad as long 7

5. Palps as long as dorsum of basis capituli, coxa I medium sized 6

Palps much longer than dorsum of basis capituli, coxa I of large size . . . . **longicoxatus.**

6. Basis capituli without a longitudinal ridge external to porose areas . . . . **sanguineus.**

Basis capituli with a longitudinal ridge external and at a tangent to the porose areas . . . . **appendiculatus.**

7. Scutum with numerous punctations 8

Scutum with about twenty large punctations . . . . . **cuspidatus.**

8. Scutum with sub-equal punctations 9

Scutum with sparsely scattered punctations of very unequal size 15

9. Scutum with large punctations close together 10

Scutum with fine punctations 13

10. Scutum with regularly distributed punctations 11

Scutum with punctations in area between cervical and lateral grooves . . . . **supertritus.**

11. Basis capituli together with palps as broad as long 12

Basis capituli together with palps longer than broad . . . **capensis.**

12. Posterior border of scutum bending up opposite the lateral grooves . . . . **bursa.**

Posterior border of scutum convex or slightly angular . . **kochi.**

13. Scutum with numerous punctations throughout . . . . **aurantiacus.**

Scutum with fewer punctations on the lateral border 14

14. Scutum with lateral grooves . . . . **ziemanni.**

Scutum with marked lateral grooves . . . . **attenuatus.**
(Congo.)

15. Scutum with no large punctations near posterior border 16

	Scutum with large punctations extending up to the posterior border	**haemaphysaloides.**
16.	Articles of legs marked with fine punctations	**17**
	Articles of leg with deep punctations, large as those on the scutum	**armatus.**
17.	Scutum with deep lateral grooves	**18**
	Scutum with lateral grooves formed of punctations	**ecinctus.**
18.	Scutum with convex or slightly angular posterior border	**simus.**
	Scutum with posterior border bending up behind the eyes	**tricuspis.**
19.	Scutum oval with a slightly sinuous contour	**pulchellus.**
	Scutum as broad as long with a sinuous contour	**maculatus.**
20.	Scutum longer than broad with widely separated punctations; legs reddish brown	**oculatus.**
	Scutum as broad or nearly as broad as long, with punctations closer together; legs reddish yellow	**evertsi.**

Rhipicephalus sanguineus, Latr. **Male.** (Plate LXXVII, figs. 1 and 2.) Scutum brown with flat eyes; basis capituli with lateral projections. Marginal grooves extending to and bounding the extreme festoons; a white margin surrounding the scutum. Punctations very unequal in size, numerous small ones evenly distributed, between which there are very large ones scattered irregularly. Adanal plates triangular, at least twice as long as broad. Anus situated about the middle of the length of the plates; accessory plates small and spiniform. Spiracles much elongated, three times as long as broad. Coxa I without anterior hump or projection. Length 3·3 mm.; width 1·5 mm. (Neumann)

Female. Scutum oval, a little longer than broad; lateral grooves limited by a clear relief, punctations numerous and unequal. Basis capituli a little broader than half the width of scutum. Porose areas small, nearly circular. Length 3 to 11 mm.; width 1·5 to 7 mm. (Neumann)

This species is found almost all over the world and is essentially the dog tick; in the United States it is found only in the extreme southern part of Texas, where it is known as the 'brown dog tick'. Neumann states it has been found on the fox, jackal, cat, lion, hare, horse, camel, and even on man. He recognizes the following varieties:—

Variety *punctissimus*, Gerstaecker. Scutum with punctations more equal and numerous. Male. Length 3 mm.; breadth 1·6 mm. Female. Length 2·7 to 8 mm.; breadth 1·5 to 6 mm. This variety is found in Zanzibar, Togo Land, Abyssinia, Natal, Cape Colony, and Walfish Bay; it is parasitic on the dog and on cattle.

Variety *brevicollis*, Neumann. Smaller than *sanguineus*; emargination of scutum less marked; legs more slender. In the female the scutum is longer; the eyes are situated a little more posteriorly than in *sanguineus*. Male. Length 2 mm.; width 1 to 1·3 mm. Female. Length 7 mm.; width 4 mm. This variety is found in Zanzibar and Nubia.

Rhipicephalus sanguineus is the invertebrate host of *Piroplasma canis*.

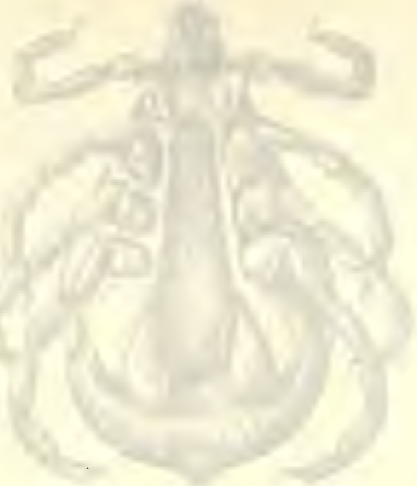
Rhipicephalus appendiculatus, Neumann. **Male.** (Plate LXXVII, fig. 5.) Scutum brown; eyes flat and elongated. Marginal festoons extending to and bounding the extreme festoons, which are triangular in shape; a white margin surrounds the scutum. Numerous short punctations, nearly all superficial, some anterior ones deep and arranged in rows. Adanal plates triangular, at least twice as long as broad; internal borders longer than the external; posterior borders oblique and slightly concave. Anus situated nearer the anterior ends of the adanal plates than the posterior; accessory plates well developed. Spiracles broad. Basis capituli nearly as long as broad, with slight lateral projections near anterior third. Coxa I with a conspicuous anterior hump or projection on the dorsal surface. Caudal appendage well developed, twice as long as broad. Length 4 mm.; width 2·6 mm. (Neumann)

Female. Scutum oval, longer than broad. Punctations numerous, small and superficial. Basis capituli a little more than half the width of the scutum. Porose areas small and circular, limited by longitudinal ridges. Length 4 to 12 mm.; breadth 2 to 7 mm. (Neumann)

This tick is found in Cape Colony, German East Africa, British East Africa and the Cameroons; it is parasitic on cattle, goats, horses and the dog. As already noted *R. appendiculatus* is the invertebrate host of *Theileria parva*, the piroplasm which causes Rhodesian Cattle Fever or East Coast Fever.

R. appendiculatus may be mistaken for *sanguineus*; it can be distinguished by noting the following points:—The punctations on the male scutum are much more regular than those of *sanguineus*; the caudal appendage is not so broad. It should, however, be remembered that the caudal appendages of these ticks are as a rule only well developed a few days after the males have fed. The appendage of *appendiculatus* is usually a prominent structure and nearly always turns downwards. The basis capituli in the female *appendiculatus* is broader than that of the female *sanguineus*. *Appendiculatus* can nearly always be recognized by noting that the first segment of the palp has a well-developed spur on its ventral and inner border, and by the hump on coxa I. Dönitz points out that many of the specimens from German East Africa are not typical, the punctations on the scutum being deeper and more thickly set, as in *R. bursa*.

Rhipicephalus simus, Koch, C. L. **Male.** (Plate LXXVII, figs. 3 and 4.)



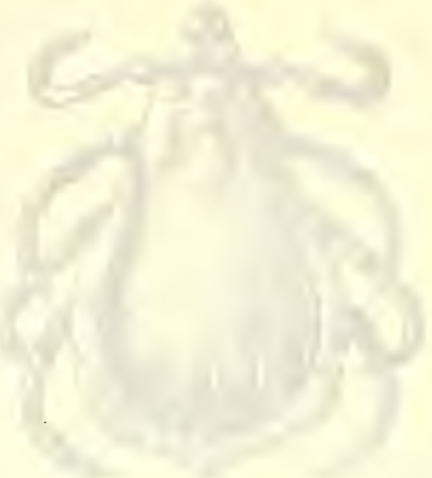
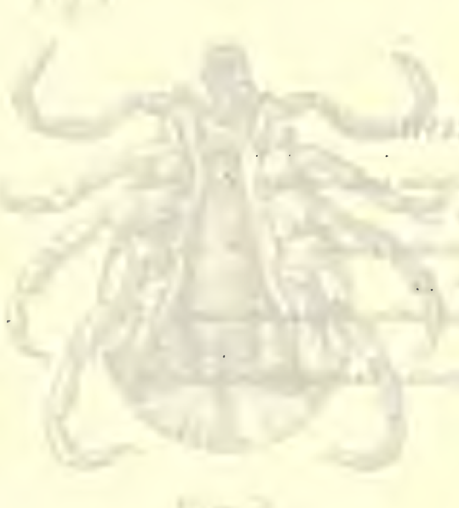


Fig. 1



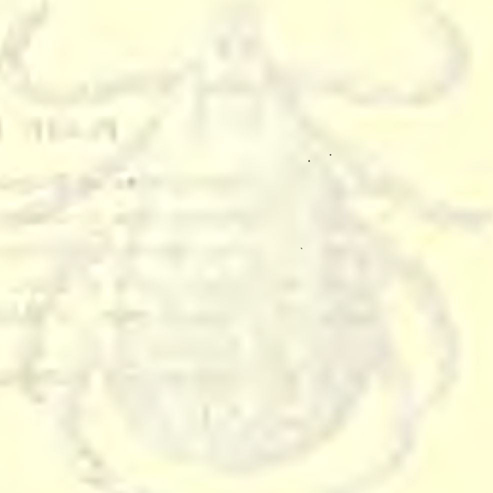


Fig. 2

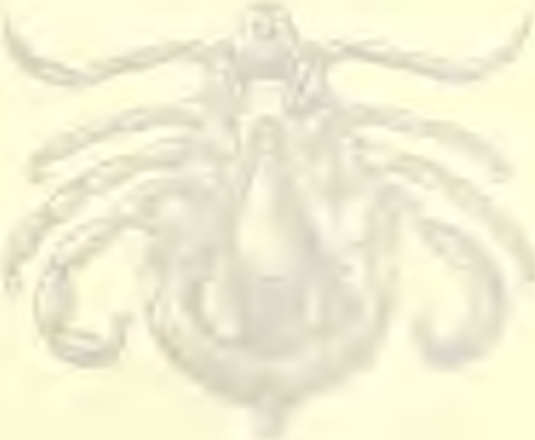


Fig. 3

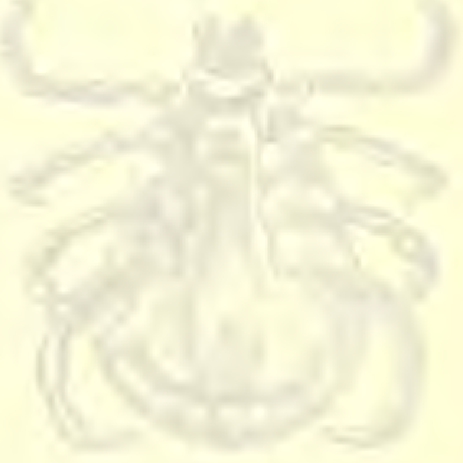


Fig. 4

PLATE LXXVII

Figure 1. Ventral view of *Rhipicephalus sanguineus*, ♂. × 22.

Figure 2. Dorsal view of same. × 22.

Figure 3. Ventral view of *Rhipicephalus simus*, ♂. × 20.

Figure 4. Dorsal view of same. × 24.

Figure 5. Ventral view of *Rhipicephalus appendiculatus*, ♂. × 12.

Figure 6. Ventral view of *Rhipicephalus haemaphysaloides*, ♂. × 18.

PLATE. LXXVII.

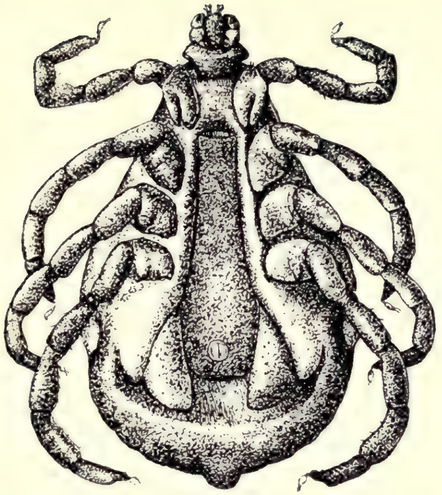


Fig. 1.

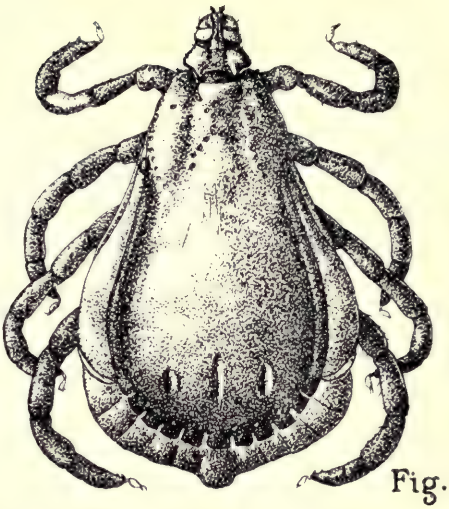


Fig. 2.

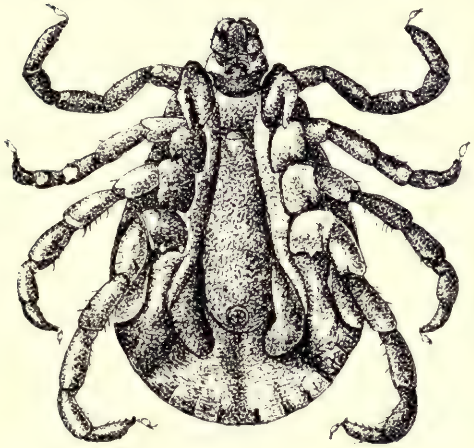


Fig. 3.

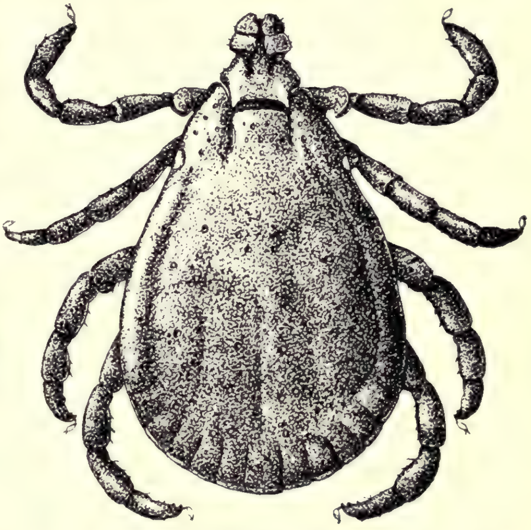


Fig. 4.

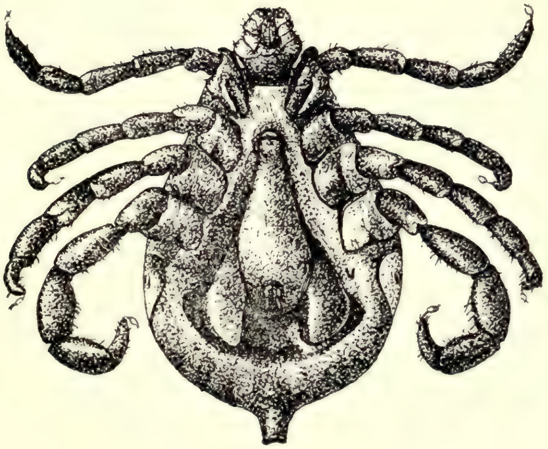


Fig. 5.

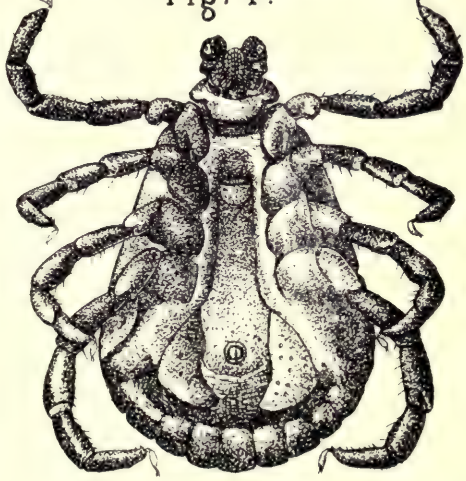


Fig. 6.

Scutum dark brown; eyes large, flat, and of a yellowish colour. The marginal groove extends to and bounds the extreme festoon. The punctations are large, equal and fairly numerous, forming longitudinal rows. Adanal plates sub-triangular, the internal borders concave, the posterior round, twice as long as broad; the anus is situated nearer the anterior than the posterior end of the plates; accessory plate elongated and spiniform. Basis capituli nearly as long as broad, lateral projections near the anterior third. Caudal appendage absent or very short. Length 4 to 6 mm.; width 2·2 to 3 mm. (Neumann)

Female. Scutum at least as broad as long, with round or slightly angular contour. Cervical grooves short and deep; lateral grooves consisting of a row of large punctations. Those on the scutum are numerous, unequal; there are fewer near the antero-lateral borders and they are absent on the posterior border. Basis capituli twice as broad as long, lateral projections at about the middle of the lateral border. Porose areas circular and of medium size, the distance between them being equal to their diameter. Length 6 to 12 mm.; width 3 to 8·5 mm. (Neumann)

R. simus is found in Egypt, Senegal, Zanzibar, Kilamanjaro, German East Africa and Madagascar; it is parasitic on cattle, also on the lion, camel, horse, zebra and dog. Neumann recognizes the following varieties.

Variety *erlangeri*, Neumann. **Male.** Scutum with marginal groove interrupted and not very deep; marked with scattered punctations neither large nor numerous, and not forming rows; this variety is found in Abyssinia.

Variety *hilgerti*, Neumann. **Male.** Scutum with marginal grooves formed anteriorly by large punctations; on the scutum itself the punctations are very fine and numerous, and are interspersed with larger ones; accessory plates obsolete; two small post-anal plates. No caudal appendage.

Female. Scutum with slightly sinous border; cervical and lateral grooves deep; punctations larger and more numerous; this variety is also found in Abyssinia, on the jackal.

Variety *planus*, Neumann. **Male.** Scutum plain with few punctations; lateral grooves broad. In the female the scutum is nearly circular in shape; lateral grooves not very deep. It is recorded from Kilamanjaro.

Variety *shipleyi*, Neumann. **Male.** Scutum with very fine punctations, not very numerous and intermixed with larger ones. Basis capituli shorter than that of the type species; lateral angles more prominent. Coxa I with longer and straighter spurs. In the female the scutum also has fine punctations. This variety is found on the hyaena in the Soudan.

Rhipicephalus simus, popularly known in South Africa, as the 'black pitted tick', is easily recognized by the somewhat indistinct median and accessory furrows near the posterior margin; the lines are almost microscopical and may be wanting in the male. The adanal plates are better developed than in *appendiculatus*. *R. simus* is the invertebrate host of *Theileria parva*.

Rhipicephalus bursa, Can. and Fan. **Male.** Scutum brown; eyes prominent; white margin surrounding the scutum; marginal groove extending to and bounding the extreme festoon. Punctations numerous, of various sizes, large, medium and small, and in mixed clusters. Adanal plates triangular, nearly twice as long as broad, posterior border round; anus situated nearer the anterior than the posterior end. Accessory plates small, triangular and spiniform. Caudal appendage absent or if present very short; spiracles elongated. Length 4·5 mm.; width 3 mm. (Neumann)

Female. Scutum as broad as long, round. Cervical grooves deep anteriorly and broader posteriorly; lateral grooves absent. Punctations numerous, thickly set and fairly equal in size. Capitulum together with palps as broad as long. Porose areas large and oval, and divergent anteriorly. Length 4 to 17 mm.; width 2 to 9 mm. (Neumann)

This species is found in Southern Europe, Africa, Cuba, Vera Cruz and Batavia; it is parasitic on cattle and on the horse, sheep, goat, pig and the dog. It is the invertebrate host of *Piroplasma ovis*. The male can be recognized by the characteristic adanal plates, which have a broad posterior margin.

Rhipicephalus capensis, Koch, C. L. **Male.** Scutum dark brown with numerous large and contiguous punctations, which form transverse ridges in the middle. Eyes flat and elongated. Marginal grooves containing large punctations. Adanal plates triangular, twice as long as broad, the internal borders much longer than the external; the internal angle truncated. Anus situated nearer the anterior ends of the plates. Accessory plates well developed and with long spines. Basis capituli nearly as long as broad, the lateral projection nearer the anterior third. No caudal appendage. Spiracles long and broad. Length 4·3 mm.; width 2·8 mm. (Neumann)

Female. Scutum as broad as long, with rounded contour; cervical grooves long and deep; lateral grooves with external edge standing out in relief. Basis capituli nearly twice as broad as long, and together with the palps it is longer than broad. Porose areas circular. Length 5 mm.; width 3 mm. (Neumann)

This species is the invertebrate host of *P. bigeminum*; it is found in Cape Colony, South East Africa, Togo Land, Cameroons, German East Africa; it is parasitic on cattle and antelopes; it has been found on the lizard *Varanus saurus*. Neumann recognizes the following variety:—

Variety *compositus*, Neumann. Scutum with more regular punctations, which are almost absent on the border and the festoons; ridges less numerous and less marked. Ventral surface glabrous. Internal border of the adanal plate concave; accessory plates only slightly chitinized. Basis capituli broader; legs more delicate. Coxa I with shorter spines. In the female there are no punctations on the border of the scutum. This variety is found in the Soudan and in German East Africa; it is parasitic on the buffalo.

Rhipicephalus evertsi, Neumann. **Male.** Scutum brown with very numerous sub-equal almost contiguous punctations. Eyes spherical and shining. Legs orange red. Marginal grooves extending to and bounding the extreme festoons. Adanal plates nearly twice as long as broad, posterior border round, internal border truncated. Anus situated nearer the anterior end; accessory plates small, triangular, spiniform and often obsolete. Caudal appendage either absent or very short. Spiracles twice as long as broad. Length 5 to 6 mm.; width 3 to 4 mm. (Neumann)

Female. Scutum as long or a little longer than broad, oval in shape; eyes situated towards the middle of the length. Cervical grooves markedly curved; no lateral grooves. Porose areas large and oval, divergent anteriorly. Length 5 to 14 mm.; width 3 to 9 mm. (Neumann)

This tick is the invertebrate host of *Piroplasma equi*; it is parasitic on the horse and on cattle in Cape Colony, the Transvaal, Togo Land and German East Africa.

Bionomics and Life Processes of Rhipicephalus

There are two distinct types of life processes to be noted in the ticks of the genus *Rhipicephalus*, one represented by *Rhipicephalus sanguineus* and the other by *Rhipicephalus evertsi*. In the first type, the commoner of the two, the tick requires three distinct hosts, but these need not necessarily be the same species of animal. The larva of *sanguineus*, the common dog tick, on becoming replete with blood leaves its host; the nymph and adult behave in the same way. The larva may feed on a dog, the nymph on a jackal and the adult on a horse. The other type of life history is exemplified by *R. evertsi*, the horse tick of South Africa. Its larva on becoming replete does not drop off but moults on the host; the nymph feeds on the same host and when replete with blood drops off; the adult attacks a second host. *Evertsi* is a general feeder, but whatever its host may be, the ticks always remain attached until the replete nymphal stage is reached. *Rhipicephalus bursa*, the sheep tick, behaves in the same way as *evertsi*, the larva remaining attached to the first host until the nymph becomes replete. *Rhipicephalus appendiculatus*, the common cattle tick of South Africa, will attack almost any warm-blooded animal in all its stages. *R. simus* and *R. capensis*, on the other hand, are peculiar. Their larvae appear to feed on some special host; the nymphs and adults are general feeders.

GENUS MARGAROPUS, KARSCH

Capitulum short, with base hexagonal on the dorsal surface, forming on each side a projecting angle. Palps short and broad. Spiracles circular or short ovals; tarsi with one or two spurs. Anal groove absent; posterior festoons wanting but in their places there are often small notches. Marginal grooves absent. Scutum chestnut brown, small and in the female with parallel sides in its anterior half. (Neumann)

The genus *Margaropus* of Neumann includes *Margaropus*, Karsch, and *Boophilus*, Curtice. Nuttall and Warburton retain the genus *Boophilus* and make *annulatus* the type species. Neumann regards *Margaropus winthemi*, Karsch, from Valparaiso, as an abnormal specimen of *annulatus*; on the other hand Dönitz, and Nuttall and Warburton, consider it to be a good species. *Boophilus* only differs from *Margaropus* in having bifid coxae and legs of normal width. Neumann gives the following key to the species of *Margaropus*:—

NEUMANN'S KEY TO THE SPECIES OF MARGAROPUS.

MALES

1.	Four adanal plates, free anterior to the anus; segments of the legs sub-cylindrical, angles at the joints slightly prominent.	**annulatus.**
2.	Two adanal plates united anterior to the anus; segments of the legs greatly dilated, angles at the joints pronounced .	**lounsburyi.**

FEMALES

1.	Segments of legs sub-cylindrical, spur short, hooks terminal; second and third segments of palps thickest in the middle, and forming a sharp angle externally	**annulatus.**
2.	Segments of legs dilated at their distal extremities, spur very long, hooks inserted on the dorsal border of the spur, and far from its point; palps with second and third segments rounded externally	**lounsburyi.**

PLATE. LXXVIII.

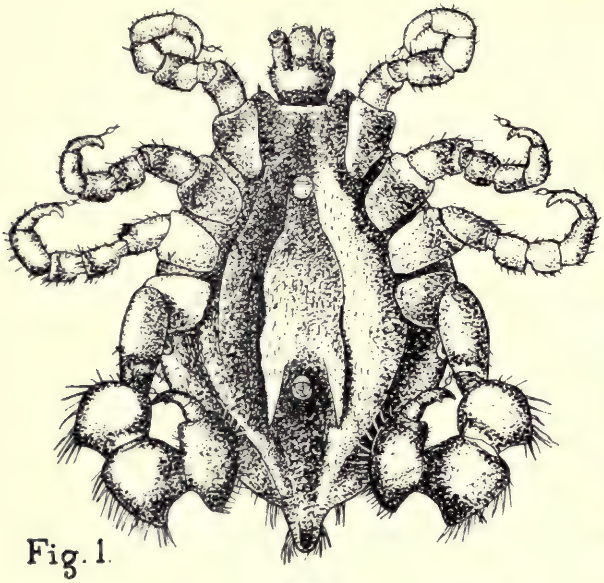


Fig. 1.

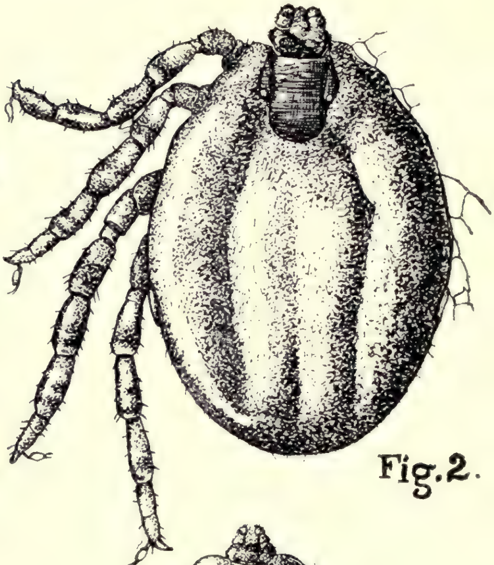


Fig. 2.

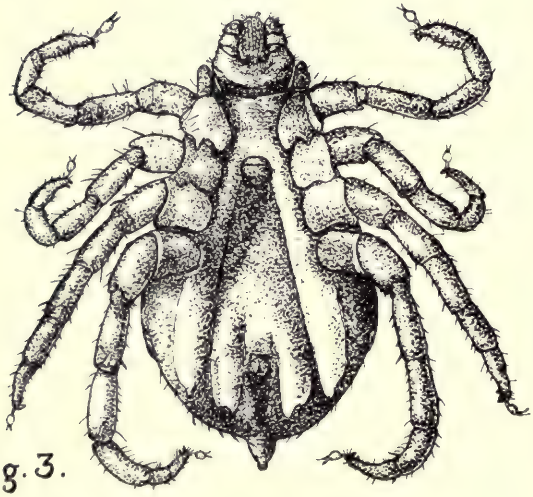


Fig. 3.

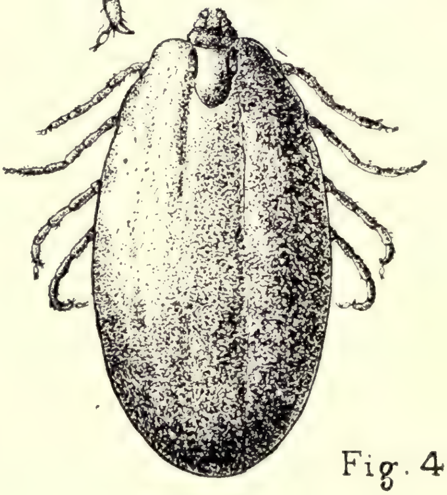


Fig. 4.

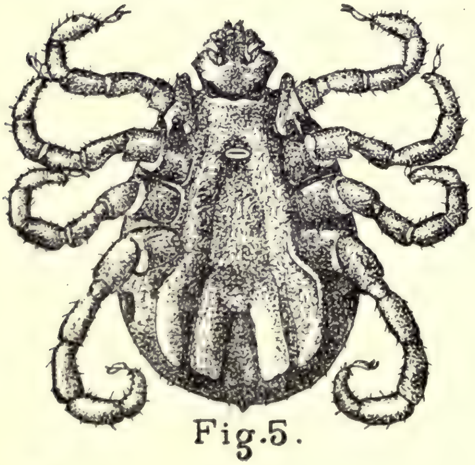


Fig. 5.

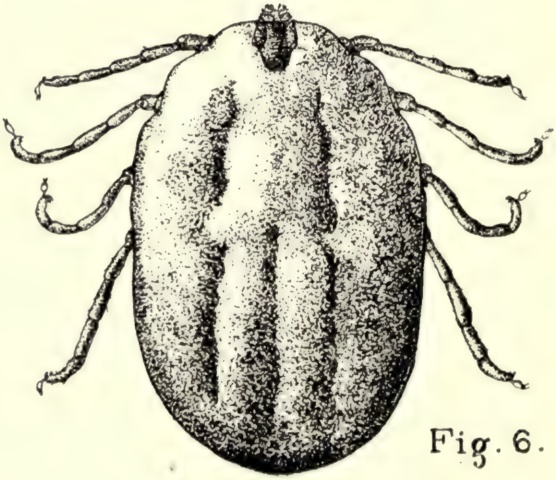


Fig. 6.

PLATE LXXVIII

Figure 1. Ventral view of *Margaropus lounsburyi*, ♂. × 17.
Figure 2. Dorsal view of ♀ of same. × 17.
Figure 3. Ventral view of *Margaropus annulatus* var. *decoloratus*, ♂. × 22.
Figure 4. Dorsal view of ♀ of same. × 10.
Figure 5. Ventral view of *Margaropus annulatus annulatus*, ♂. × 22.
Figure 6. Dorsal view of ♀ of same. × 12.

PLATE XXVII.

Margaropus annulatus, Say. **Male.** (Plate LXXVIII, fig. 5.) Second and third segments of palp thinnest in the middle, forming a sharp angle externally. Hypostome with eight rows of teeth. Segments of legs sub-cylindrical; spurs short; hooks sub-terminal. Adanal plates free anteriorly, rectangular or sub-triangular in shape; internal border longer than the external; posterior border oblique; accessory plate similar but smaller and usually triangular in shape. Caudal appendage absent. Coxa I has two spurs and an anterior hump or projection visible from the dorsal surface. Length 2·15 to 2·35 mm.; width 1·3 mm. (Neumann)

Female (fig. 6.) Body as broad in front as behind, slightly constricted in the middle. Porose areas large and oval, broader than long. Maximum length 13 mm.; maximum width 7·5 mm. (Neumann)

Neumann recognizes the following varieties:—*australis*, *calcaratus*, *decoloratus*, *caudatus* and *argentinus*.

Variety *australis*, Fuller. Hypostome with eight rows of teeth. Male with a well-developed caudal appendage; adanal plates more chitinous, rectangular and straighter. The female has a shorter scutum and the eyes are nearer the middle of its length; porose areas short. Length 10 to 11 mm.; width 6 to 7 mm. (Neumann) This variety is found in Australia, the Philippine Islands, the Antilles, Guatemala, Venezuela, Guiana, Brazil, Argentine Republic, Paraguay and Uruguay. It is parasitic on cattle, horses and dogs.

Variety *calcaratus*, Birula. Hypostome with eight rows of teeth. Male without a caudal appendage; adanal and accessory plates straighter and less chitinous than in the type. Female with scutum shorter and straighter; eyes nearer the middle of the length of the scutum. Porose areas oval, broader than long. Body relatively straight and long when replete. *Calcaratus* is found in Algeria, Tunis, Egypt, Abyssinia, Roumania and the Caucasus; it is parasitic on cattle, horses and sheep.

Variety *decoloratus*, Koch, C.L. Male (Plate LXXVIII, fig. 3) with caudal appendage well developed; adanal and accessory plates pointed on their postero-internal borders. Hypostome with eight, sometimes six, rows of teeth. Female with scutum smaller than in the type; porose areas also smaller. Hypostome with six, often eight rows of teeth. *Decoloratus* is found in Cape Colony, Natal, Transvaal, Maurice Island, Demaraland, Benin, Gabon, Cameroon and Togo Land; it is parasitic on cattle, horses, sheep and goats.

Variety *caudatus*, Neumann. Hypostome with eight to ten rows of teeth. Male with caudal appendage well developed; adanal plates indented on their posterior borders; accessory plates pointed on their postero-internal borders. Female with scutum small and short; eyes situated a little anterior to its middle. Porose areas sub-circular. It is found on the horse in Japan.

Variety *argentinus*, Neumann. Hypostome in female with six rows of teeth; scutum and capitulum small; porose areas elongated transversely. Legs relatively short. Male unknown. This variety is found in Buenos Ayres.

Margaropus lounsburyi, Neumann. **Male.** (Plate LXXVIII, fig. 1.) Palps with second and third segments not forming an external projection. Legs with well-developed long, broad segments; claws inserted at a distance from the spur. Hypostome with eight rows of teeth. Adanal plates straight and awl-like, joining each other anterior to the anus to form an uneven plate. Accessory plates wanting. Caudal appendage well marked, and bearing tufts of hairs. Coxa I undivided, with two very small spurs; on each of the other coxae there is a small spur. Legs increase in size from before backwards; the segments of leg IV are greatly dilated and form deep angles. Length 3·9 to 4·3 mm. (Neumann)

Female (fig. *2*). Body a little broader in front than behind. Porose areas large and oval, twice as long as broad. Legs with cylindrical segments, dilated at their distal extremities. Maximum length 16 mm.; maximum width 10 mm. This tick is found in Cape Colony and the Orange River Free State, on cattle and horses.

Relation to Disease: Life Processes

Ticks of the genus *Margaropus* are of considerable importance, for *annulatus, australis* and *decoloratus* are the invertebrate hosts of *Piroplasma bigeminum*; *decoloratus* in addition transmits *Spirocahaeta theileri* to cattle. *P. bigeminum* penetrates the egg of the tick and the larvae which hatch out later are infected with the parasite; they, as well as the nymphs, are infective. It is very probable that parasites ingested by the larvae are transmitted later by the adults.

The life processes of the ticks of the genus *Margaropus* differ from those of the rhipicephalines, such as *evertsi* and *bursa*, which only have two hosts, as they pass their complete life histories on one animal, the nymph and females remaining at the same spot at which the larvae attached themselves; the males, however, move about in search of the females. As far as is known all the varieties of *annulatus* described above behave in the same way.

GENUS HYALOMMA, KOCH, C. L.

Capitulum long with rectangular base and without lateral angles. Palps and hypostome long; spiracles comma-shaped. Anal groove present. Coxa I bidentate. (Neumann)

Neumann gives the following key to the species :—

NEUMANN'S KEY TO THE SPECIES OF HYALOMMA

MALES

1. Scutum dark brown 2
   Scutum light yellow, with dark punctations, and decided markings . . . . **hippopotamense.** (South Africa.)
2. Coxa I deeply bidentate; internal border of adanal plates longer than the posterior border 3
   Coxa I not deeply bidentate; internal border of adanal plate shorter than the posterior border. . . . . . . **syriacum.**
   (Syria; Asia Minor; Algeria; Tunis; Tripoli; Egypt; Greece; Athens; Roumania; Russia; Senegal; Congo.)
3. Scutum with numerous deep punctations, lateral groove present . . . . **aegyptium.**
   Scutum with few punctations, which are superficial, no lateral groove . . . . **rhipicephaliodes.** (Egypt.)

FEMALES

1. Scutum dark brown 2
   Scutum pale yellow, with dark punctations, and decided markings . . . . **hippopotamense.**
2. Coxa I deeply bidentate, scutum as broad or a little broader than long with numerous punctations . . . . **aegyptium.**
   Coxa I not deeply bidentate, scutum a little longer than broad, with punctations less numerous . . . . **syriacum.**

Hyalomma aegyptium, **Male.** (Plate LXXII, figs. 1 and 3.) Scutum brown, with numerous unequal punctations; eyes spherical. Hypostome spatulate with six rows of teeth. Coxa I divided into two long spurs. Adanal plates rectangular, the internal border much longer than the posterior; accessory plates small and rectangular. Scutum with a short lateral groove close to the border, extending to and bordering the external festoon, which is more or less indistinct. Length 6 to 7 mm.; width 3·5 to 5 mm. (Neumann)

Female. Scutum oval, hexagonal, with sinuous borders, as broad or a little broader than long, with lateral grooves. Length 7 to 20 mm.; width 3·5 to 18 mm. (Neumann)

This species is widely distributed; it occurs in Algeria, Sahara, Tunis, Egypt, Abyssinia, East Africa, Senegal, Loango, Cape of Good Hope, Asia Minor, Persia, East Turkistan, Mongolia, India, Sardinia, Italy, Sicily, Spain, Greece, Roumania, and Hertzgovinia. It is parasitic on cattle, the buffalo, camel, rhinoceros, horse, giraffe, sheep, goat, antelope, pig, dog, cat, and hare, and occasionally bites man.

Neumann recognizes three varieties, as follows:—

Variety *dromedarii*, Koch, C.L. Male scutum with moderately deep punctations, not so light as in the type. Ventral surface and median festoon of a whitish colour; adanal and accessory plates well developed and pointed towards the median line posterior to the anus. It is found in Syria, Egypt and Bokhara; it is parasitic on the camel.

Variety *lusitanicum*, Koch, C.L. Scutum not so dark as in type; eyes very black, legs whitish on their dorsal and ventral borders, and with dark punctations; it is found in Portugal.

Variety *impressum*, Koch, C.L. Scutum dull with numerous contiguous and equal punctations.

As far as is known at present all ticks of the genus *Hyalomma* require three hosts in order to complete their life processes; *Hyalomma aegyptium*, however, is peculiar in its habits, as its larvae do not feed on the same species of host as the adults. During the course of the examination of more than 3,000 calves used for purposes of vaccination at the King Institute, the larva of *Hyalomma aegyptium* has never been found on a single animal; the nymph was found twenty-four times, while the adults are present on almost every calf brought to the Institute. In addition the adults have been taken from horses and dogs, and are very common on the South Indian hare, *Lepus nigricollis*, attaching themselves about the ears and neck. On cattle they are always found in the region of the udder or scrotum; they remain attached for long periods and when in large numbers cause sores which render the animals unsuitable for vaccination. In 1908 the senior author carried out a long series of experiments with this tick to determine the particular host or hosts it feeds on. Large numbers of larvae were bred out of eggs laid by females in the laboratory, and these were placed on the following animals:—Calf, sheep, goat, pig, dog, cat, rabbit, guinea pig, rat, and pigeon; although a few larvae attached themselves to guinea pigs and rats, they refused to feed on the other animals. The experiments were repeated but without success. It is possible that the palm squirrel, *Funambulus palmarum*, and the hare, *Lepus nigricollis*, are the hosts of the larvae; nymphs have been

Bionomics and Life Processes of Hyalomma aegyptium

found on the squirrel. It is, however, certain that the larvae do not attach themselves to any of the common domestic animals in Madras. Lounsbury has had very similar experiences in South Africa.

In a recent paper Nuttall states that the larvae of *Hyalomma aegyptium* will feed on the ram, hedge hog and guinea pig, and he has raised all the stages on these animals; it is doubtful, however, whether these animals are the natural hosts.

TRIBE AMBLYOMMATARIA

Anal groove contouring the anus posteriorly, with limbs directed forwards and joining the genital grooves at the level of the spiracles; anal groove sometimes absent. Palps hollowed out on their internal surfaces; eyes present or absent. Usually eleven festoons on the posterior border. Scutum often highly ornamented with light spots. Shields absent on the ventral surface of the male. (Neumann)

Neumann gives the following key for the determination of the genera :—

NEUMANN'S KEY TO THE GENERA OF AMBLYOMMATARIA

1.	Eyes present	2
	Eyes absent	3
2.	Capitulum long; coxa IV of male slightly larger than the other coxae	**Amblyomma.**
	Capitulum short; coxa IV of male markedly larger than the other coxae	**Dermacentor.**
3.	Capitulum long, second segment of palp not humped externally	**Aponomma.**
	Capitulum short, second segment of palp humped externally	**Haemaphysalis.**

GENUS AMBLYOMMA, KOCH, C. L.

Eyes flat, sometimes spherical; capitulum long with rectangular base; lateral borders without humps or projections. Palp with the second segment long and without any external processes. Scutum often highly ornamented with light coloured patches. Spiracles usually triangular and with rounded angles. Posterior border nearly always with eleven festoons (at least in the male). Males without adanal plates but often with ventral plaques (Dönitz) close to the festoons. Coxa IV of the male slightly larger than the other coxae. (Neumann)

Ticks of the genus *Amblyomma* are chiefly found in tropical and sub-tropical countries; up to the present not a single species has been recorded from Europe. North and South America and Africa are specially rich in species; a few are found in Asia. The majority are parasites of wild animals; some are found on domestic animals and several species occur on birds, and a few on reptiles. Except for *Amblyomma hebraeum* the other species are of little or no practical importance.

Dönitz has pointed out that the males of *Amblyomma* often have small ventral plates in front of the festoons. These plates, however, differ from those of *Hyalomma* and *Rhipicephalus* in that they are deeply embedded in the integument and are quite immovable; Dönitz believes that they are not homologous with the true anal plates of the two genera mentioned above.

Neumann gives the following key for the determination of the species:—

Neumann's Key to the Species of Amblyomma

Males

1.	Eyes flat, not prominent	2
	Eyes spherical	53
2.	Scutum with marginal groove completely contouring the posterior border	3
	Scutum with no marginal groove or an incomplete one	20
3.	Coxa I without long sub-equal, conical, contiguous spurs	4
	Coxa I with two very long, sub-equal, conical, and contiguous spurs	19
4.	Coxa I with two spurs or simple tuberosities	5
	Coxa I with one long spur	**maculatum**. (United States; California; Texas; Tennesse; Mexico; Brazil; Peru; Paraguay; Uruguay; Argentine Republic; Chili; Patagonia.)
5.	Coxa IV with a spur as long or nearly as long as the coxa	6
	Coxa IV with spur much shorter than that article	8
6.	Scutum without punctations on the triangular projections, shallow and radiating in posterior half	**cajennense**. (Central and South America; Cuba; Jamaica.)
	Scutum with punctations distributed over its entire surface	7
7.	Coxa IV with a spur slightly longer than the coxa; capitulum long with short base	**americanum**. (United States; Guatemala; Brazil.)
	Coxa IV with a spur twice as long as the coxa; capitulum short with long base	**neumanni**. (Argentine; Patagonia.)
8.	Coxa IV with a spur half the length of the coxa	9
	Coxa IV with a very short spur	10
9.	Coxa I with two strong equal spurs	**coelebs**. (Bolivia.)
	Coxa I with an external spur double the length of the internal	**crenatum**. (Cape of Good Hope; Liberia; South India.)

10. Coxa I bidentate 11
Coxa I with a single spur, body elongated, scutum with longitudinal markings . . . . **longirostra**.
(Brazil ; Venezuela ; Trinidad)

11. Ventral surfaces of festoons not prolonged posteriorly 12
Ventral surfaces of festoons prolonged by an entire membrane **prolongatum**.
(South India ; Ceylon.)

12. Scutum with marginal swellings, smooth or punctate 13
Scutum with marginal swellings longitudinally striated . . **triguttatum**.
(Australia.)

13. Scutum without longitudinal postero-median dark bands 14
Scutum with longitudinal postero-median dark bands 17

14. Scutum uniform brown . . . . **concolor**.
(Brazil ; Argentine.)
Scutum dark with light markings, or light with dark markings . . . 15

15. Scutum dark with light markings 16
Scutum light bordered with brown . . . . . . **clypeolatum**.
(West Indies.)

16. Scutum with punctations, large, unequal, and covering the whole surface . . . . **geayi**.
(Brazil ; Guava ; Columbia.)
Scutum without punctations in the centre, very few on the festoons . . . . **sparsum**.
(Algeria ; French Guinea.)

17. Scutum light at the sides . . . . **marmoreum**.
(Cape Colony ; Mozambique ; German East Africa ; Zanzibar ; Congo ; Senegal.)
Scutum dark at the sides 18

18. Scutum with very short fine punctations . . . . . **hebraeum**.
Scutum with large deep punctations, close together, and confluent in parts . . . . **loculosum**.
(Island of Cargados Carajos.)

19. Coxa IV with a spur much shorter than the coxa . . . **fossum**.
(Costa Rica ; Buenos Ayres.)
Coxa IV with a spine as long or nearly as long as the coxa . **ovale**.
(Mexico.)

20. Scutum with incomplete marginal groove (formed of punctations or not contouring the posterior border) 21
Scutum without marginal groove 27

21. Festoons not prolonged by a membrane 22
Festoons prolonged by a membrane . . . . . **incisum**.
(Bolivia.)

22. Coxa I with two long spurs . . . . **striatum**.
(Brazil ; Paraguay.)
Coxa I with two short spurs 23

23. Scutum with marginal groove continuous 24
Scutum with a light border, and marginal groove formed of punctations 26

24. Body very straight, anteriorly with sub-rectangular sides . **cuneatum**.
(Congo ; Uganda ; Togo Land ; Cameroon.)
Body broad with convex sides 25

25. Scutum with reddish yellow patches, marginal grooves commencing posterior to the eyes . . . **moreliae**.
(Australia.)

Scutum coloured brown, marginal grooves commencing on a level with the eyes . . . **australiense**.
(Eastern Australia.)

26. Scutum with broad border interrupted, festoons with very fine punctations . . . **limbatum.**
(King Island; Australia; Adelaide.)

Scutum with uninterrupted straight border, festoons with very large punctations . . . **albolimbatum**.
(Eastern Australia.)

27. Coxa I with two short spurs . . . 28
Coxa I with two long spurs . . . 50

28. Coxa IV has one or two spurs shorter than the coxa . . . 29
Coxa IV has one spur longer than the coxa . . . **multipunctum**.
(Venezuela; North America.)

29. Scutum with very marked punctations . . . 30
Scutum nearly smooth, punctations nearly all very fine . . . 46

30. Coxa IV has one spur or tuberosity . . . 31
Coxa IV has two short spurs, not longer than broad . . . 44

31. Coxa IV has one spur twice as long as broad . . . 32
Coxa IV has one spur or tuberosity very little or no longer than broad . . . 34

32. Hypostome with six rows of teeth . . . **dissimile.**
(Mexico; Antilles; Columbia; Venezuela; Guiana; Brazil; Paraguay; Philippine Islands.)
Hypostome with eight rows of teeth (Africa) . . . 33

33. Scutum with transverse brown marks; coxa I has an external spur three times as long as broad . . . **personatum**.
(German East Africa.)

Scutum with longitudinal brown marks; coxa I with an external spur four times as long as broad . . . **petersi**.
(German East Africa; Mozambique; Madagascar; Liberia.)

34. Coxa I has two strong equal spurs longer than broad . . . 35
Coxa I has a small internal spur . . . 36

35. Scutum short (4 mm.) and broad without markings . . . **goeldi**.
(Brazil; Guinea.)

Scutum long (7 mm.), straight with yellow markings . . . **pictum.**
(Brazil.)

36. Coxa I has two short equal spurs . . . 37
Coxa I has two unequal spurs or tuberosities . . . 41

37. Scutum with light markings . . . 38
Scutum without markings, but with whitish border . . . **fuscum**.
(South America.)

38. Scutum without prominences . . . 39
Scutum with prominences . . . 40

39. Scutum equally ornamented throughout and with punctations evenly distributed . . . **scutatum.**
(Guatemala; Brazil; Paraguay.)

Scutum with markings and punctations especially at its periphery . . . . **albopictum**.
(Cuba; Brazil.)

40. Coxa II and III with two spurs . . . . **cruciferum.**
(Hayati.)

Coxa II and III flat, and one with spur . . . . . **malayanum**.
(Singapore.)

41. Scutum with punctations on the whole surface **42**

Scutum with punctations absent in places; tarsi gradually attenuated . . . . **cyprium.**
(New Guinea; Malay; Philippine Islands.)

42. Tarsi attenuated and indented; hypostome with eight rows of teeth . . . . **testudinarum**.
(South India; Ceylon; Java; Sumatra; Borneo; Annam.)

Tarsi gradually attenuated **43**

43. Coxa I with weakly developed spurs; hypostome with six rows of teeth . . . . **decoratum**.
(Java; Sumatra; Philippine Islands.)

Coxa I with well-developed external spur; hypostome with eight rows of teeth . . . . **scaevola**.
(New Guinea.)

44. Coxa IV with distinct spurs; body without hairs or with short hairs at the sides **45**

Coxa IV with weak spurs, and long hairs at the sides of the body . . . . **hirtum.**
(Galapagos Islands; Island of St. Paul.)

45. Scutum with whitish spots on scapular angles . . . . . **humerale.**
(Brazil.)

Scutum without whitish spots on scapular angles . . . **argentinae.**
(Argentine.)

46. Festoons without spines on their ventral surfaces **47**

Festoons (except the external one) with a ventral spine . . **naponense**.
(Equator, River Napo.)

47. Coxae II, III, and IV with two short flat spurs . . . . **tuberculatum**.
(Florida; Cuba.)

Coxae II, III, and IV with a single spur. **48**

48. Coxa I with two equal spurs as broad as long **49**

Coxa I with the external spur double the internal . . . . **tholloni**.
(German East Africa; Congo; Cameroon.)

49. Body sub-triangular . . . . **fulvum**.
(Brazil.)

Body short and oval . . . . **sub-laeve**.
(Java; Sumatra; Siam; China.)

50. Coxa IV with a spur as long as the coxa . . . . . **calcaratum**.
(Brazil.)

Coxa IV with a spur much shorter than the coxa **51**

51. First article of palp without a ventral retrograde hump **52**

First article of palp with a ventral retrograde hump . . **nodosum**.
(Costa Rica; Brazil.)

52. Hypostome with eight rows of teeth; coxa IV with a spur much longer than broad . . . . **guianense**.
(Guiana.)

Hypostome with six rows of teeth ; coxa IV with a short spur . . **varium**.
(Brazil ; Para ; Argentine.)

53. Scutum with marginal groove complete, contouring the posterior border **54**
Scutum without marginal groove, or only formed of punctations, not contouring the posterior border . . . . . **sylvaticum**.
(Cape of Good Hope.)

54. Palps short ; coxa IV with a long spur . . . . . . **parvitarsum**.
(Bolivia ; Chili.)
Palps long ; coxa IV with a short spur . . . . . . **variegatum**.
(Abyssinia ; German East Africa ; Zanzibar ; Madagascar ; Reunion ; Angola ; Congo ; Togo Land ; Benin ; Ivory Coast ; Senegal ; Antigua ; Guatemala.)

FEMALES

1. Eyes flat not prominent **2**
Eyes spherical, prominent and orbicular or sub-orbicular **57**
2. Coxa I with two spurs **53**
Coxa I with one spur **56**
3. Coxa I with unequal spurs **4**
Coxa I with equal or sub-equal spurs **22**
4. Scutum as broad or not as broad as long **5**
Scutum much longer than broad **21**
5. Scutum as broad as long **6**
Scutum much broader than long **18**
6. Scutum triangular **7**
Scutum cordiform, postero-lateral borders convex **11**
7. Scutum of medium size (2 to 3·5 mm. long) **8**
Scutum very large (5 mm. long) with confluent punctations in the scapular angles . . . . **crenatum**.
8. Scutum brown or marked with lighter spots **9**
Scutum yellow with dark spots . . . . **distinctum**.
(Ceylon.)
9. Eyes towards the anterior fourth of the scutum **10**
Eyes at plane of, or behind anterior third of scutum ; a whitish spot in the posterior angle . . . . **americanum**.
10. Coxa I with spurs much longer than broad, legs slender . . **cajennense**.
Coxa I with spurs, the internal as broad as long, legs thick and strong . . . . **hebraeum**.
11. Scutum medium size (2 to 3·5 mm. long) **12**
Scutum very broad (5 mm. long) **17**
12. Hypostome with eight rows of teeth **13**
Hypostome with six rows of teeth . . . . **decoratum**.
13. Coxae II, III, and IV with or without one spur **14**
Coxa II with two tuberosities . . . . **acutangulatum**.
(Island of Veti-Leon.)
14. Coxae II, III, and IV with one spur **15**
Coxae II and III without spurs (Africa) . . . . **tholloni**.
15. Porose areas with prominent borders, and as large as the eyes. **triguttatum**.
Porose areas without prominent borders, smaller than eyes **16**
16. Scutum without spots, lateral grooves fine, and formed of punctations . . . . **australiense**.

	Scutum with five light spots, without lateral grooves	**limbatum**.
17.	Scutum with marginal and median spots	**personatum**.
	Scutum with fairly numreous marginal spots	**petersi**.
18.	Scutum triangular	**19**
	Scutum cordiform, postero-lateral margins convex	**cordiferum**. (Banda Island.)
19.	Coxae II, III and IV with one spur	**20**
	Coxae II, III and IV with two short spurs	**sabanerae** (Guatemala.)
20.	Scutum large (4 mm. width), tarsi narrowing abruptly with dorsal receding humps	**testudinarum**.
	Scutum small (2 mm. in width), tarsi narrowing gradually	**postoculatum**. (King Island.)
21.	Scutum lozenge-shaped	**longirostre**.
	Scutum triangular	**integrum**. (Ceylon.)
22.	Coxa I with short spurs	**23**
	Coxa I with very long spurs close together	**47**
23.	Scutum as broad or hardly broader than long	**24**
	Scutum much broader than long	**39**
24.	Scutum triangular	**25**
	Scutum heart-shaped or pentagonal, with convex postero-lateral borders	**32**
25.	Hypostome with six rows of teeth	**26**
	Hypostome with eight rows of teeth ; coxae II and III without spurs	**extraoculatum**. (Singapore.)
26.	Scutum marked with spots	**27**
	Scutum uniform brown	**31**
27.	Tarsi tapering gradually	**28**
	Tarsi tapering abruptly	**30**
28.	Coxae II and III with short spurs	**29**
	Coxae II and III with one very short spur	**dubitatum**. (Southern Spain.)
29.	Scutum with about thirty large punctations	**dissimile**.
	Scutum with numerous large punctations	**supinoi**. (Burma.)
30.	Scutum with fairly numerous punctations	**marmoreum**.
	Scutum with large deep punctations, confluent in parts	**loculosum**.
31.	Tarsi narrowing abruptly ; eyes towards the anterior third of the scutum	**cuneatum**.
	Tarsi attenuated abruptly ; eyes towards the anterior fourth of the scutum	**pilosum**. (Galapagos Islands.)
32.	Tarsi gradually attenuated	**33**
	Tarsi abruptly attenuated	**35**
33.	Scutum with light markings	**34**
	Scutum uniformly brown	**concolor**.
34.	Coxae II, III and IV with one spur longer than broad	**albolimbatum**.
	Coxae II, III and IV with two spurs as broad as long	**goeldi**.
35.	Hypostome with six rows of teeth	**36**
	Hypostome with eight rows of teeth	**38**

36. Coxa I with an internal spur longer than broad; scutum with large punctations . . . . **coelebs**.
Coxa I with internal spur broader than long **37**

37. Scutum with numerous deep unequal punctations over the whole surface (most of them large) . . . . . . **geayi.**
Scutum with median punctations . . . . **argentinae**.

38. Coxae II and III with two flat, blunt spurs, a little broader than long . . . . **tuberculatum**.
Coxae II and III with one flat blunt spur twice as broad as long. **zeylanicum**. (Ceylon)

39. Without accessory dorsal plates **40**
One accessory plate posterior to scutum . . . . . . **malayanum**.

40. Coxae II. III and IV with one spur or tuberosity **41**
Coxae II, III and IV with two tuberosities, not well marked, body covered with numerous long hairs . . . . . **hirtum**.

41. Tarsi gradually attenuated **42**
Tarsi abruptly terminated; scutum uniformly brown, punctations mostly very fine . . . . **sublaeve**.

42. Scutum with clear markings **43**
Scutum uniform brown with unequal punctations . . . **deminutivum**. (Ceylon, Colombo.)

43. Eyes towards the anterior third of scutum, or more posterior **44**
Eyes towards the anterior fourth of scutum . . . . . **geoemydae**. (Sumatra; Borneo.)

44. Hypostome with eight rows of teeth **45**
Hypostome with six rows of teeth . . . . **scutatum**.

45. Capitulum nearly as long as the scutum **46**
Capitulum much shorter than the scutum, porose areas as large as the eyes . . . . **moreliae**.

46. Coxae II, III and IV with a pointed spur as broad as long . **cyprium.**
Coxae II, III and IV with one tuberosity . . . . . **breviscutatum**. (Congo.)

47. Coxa I with spurs shorter than the trochanter **48**
Coxa I with spurs as long as the trochanter **54**

48. Scutum heart-shaped, convex postero-lateral borders **49**
Scutum triangular **53**

49. Eyes towards the middle of length of scutum **50**
Eyes towards the anterior third of the scutum **51**

50. Scutum as broad as long, with a postero-median spot . . . **calcaratum**.
Scutum broader than long, with lateral spots . . . . . **nodosum.**

51. Scutum as broad as long; hypostome with eight rows of teeth **scalpturatum**. (Brazil.)
Scutum broader than long **52**

52. Hypostome with eight rows of teeth . . . . **guianense**.
Hypostome with six rows of teeth . . . . **bispinosum.**

53. Scutum as broad as long, eyes in front of the anterior third . **pictum**.
Scutum broader than long, eyes behind anterior third . . **fossum**.

54. Scutum heart-shaped with postero-lateral borders convex **55**
Scutum triangular, and as broad as long . . . . **oblongoguttatum**. (Bolivia.)

PLATE. LXXIX.

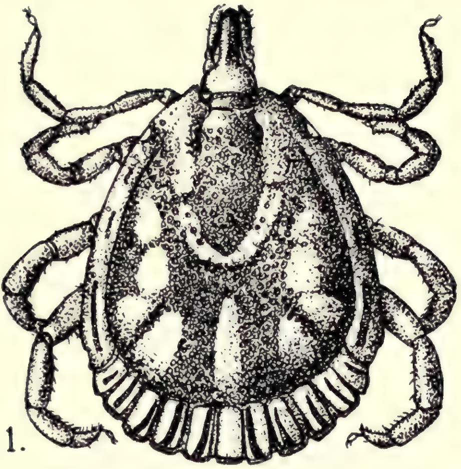


Fig. 1.

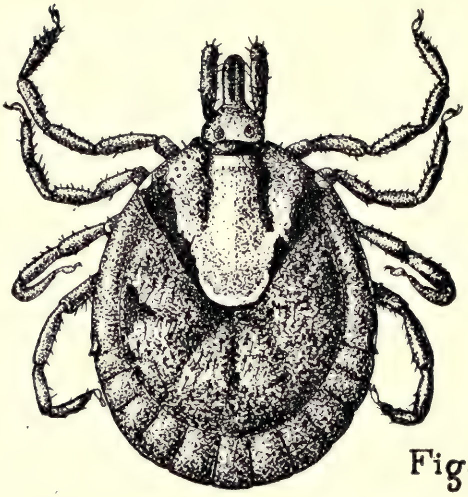


Fig. 2.

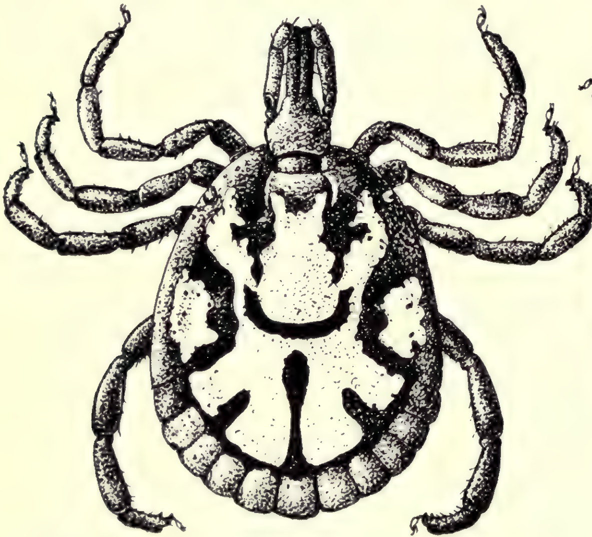


Fig. 3.

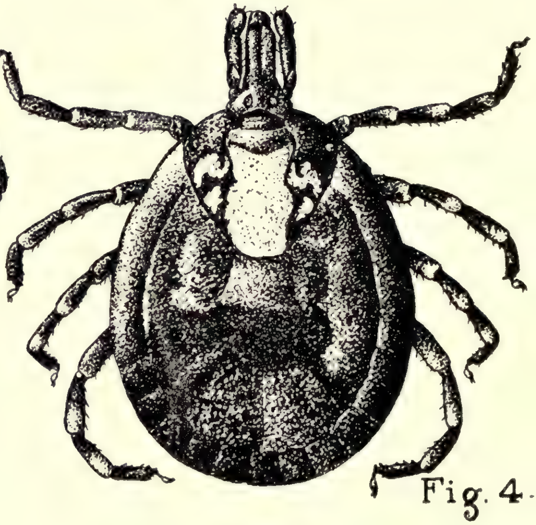


Fig. 4.

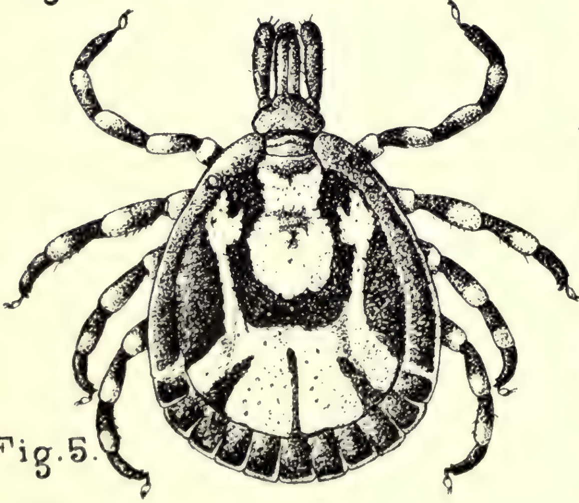


Fig. 5.

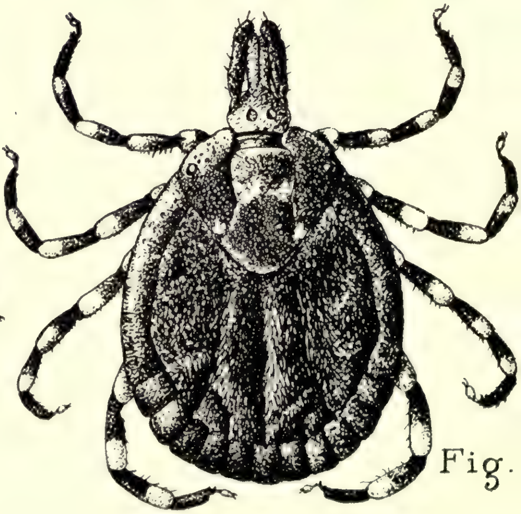
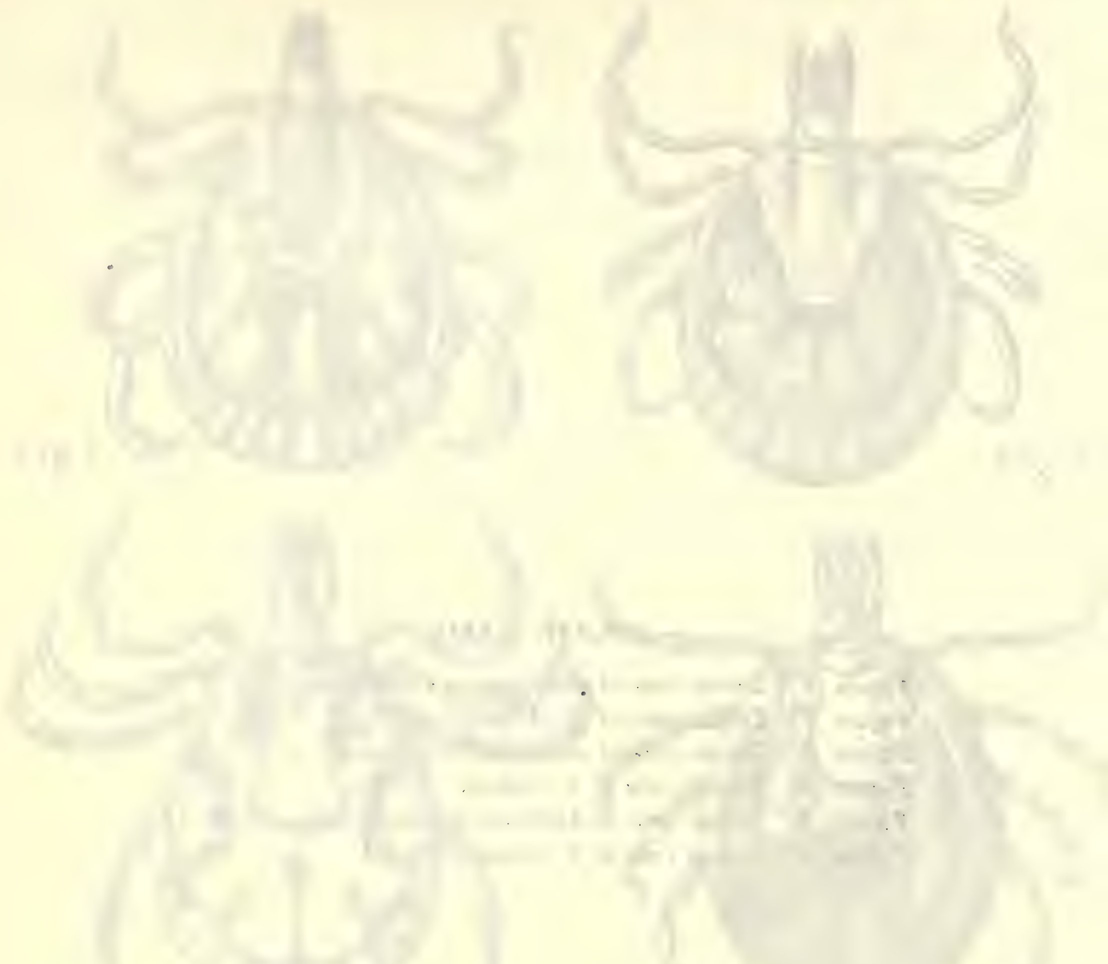


Fig.

PLATE LXXIX

Figure 1. Dorsal view of *Amblyomma cajennense*, ♂. × 12.
Figure 2. Dorsal view of ♀ of same. × 12.
Figure 3. Dorsal view of *Amblyomma hebraeum*, ♂. × 10.
Figure 4. Dorsal view of ♀ of same. × 10.
Figure 5. Dorsal view of *Amblyomma variegatum*, ♂. × 12.
Figure 6. Dorsal view of ♀ of same. × 10.

PLATE LXXXIX



55. Scutum with sub-equal and distant punctations, with extensive clear patches . . . . **striatum**.
Scutum with very unequal punctations, confluent in places, markings restricted . . . . **varium**.
56. Coxa I with very long spur ; scutum longer than broad . . **maculatum**.
Coxa I with one spine as broad as long ; scutum broader than long . . . . **latiscutatum**. (East Indies.)
57. Tarsi gradually attenuated ; scutum with postero-lateral borders concave . . . . **parvitarsum**.
Tarsi abruptly terminating ; scutum with postero-lateral borders straight or convex **58**
58. Scutum triangular, dark brown, with or without posterior spot **variegatum**.
Scutum heart-shaped, yellow with brown markings . . . **sylvaticum**.

Amblyomma cajennense, Fabr. **Male.** (Plate LXXIX, fig. 1) Scutum reddish brown with yellowish white patches, most of which are longitudinal ; punctations of medium size and absent from the scapulae. Coxa I has two short unequal conical spurs, the external the longest. Coxa IV with a spur as long as the coxa. Hypostome with six rows of teeth. Length 4·9 mm ; width 3 mm. (Neumann)

Female. (Fig 2.) Scutum triangular, a little broader than long ; eyes situated towards the anterior fourth of length of scutum ; numerous small and equal punctations. Coxa IV has a small pointed tuberosity. Length 5·5 to 14 mm ; width 3 to 11 mm. (Neumann)

This species is found in Mexico, Yucatan, Guatemala, Central America, Honduras, Nicaragua, Costa Rico, Cuba, Jamaica, Trinity, Panama, Columbia, Venezuela, Guiana, Brazil, Paraguay and the Argentine Republic ; it is parasitic on cattle, the horse and dog, and sometimes attacks man.

Amblyomma americanum, L. **Male.** Scutum reddish brown with yellowish white markings and numerous equal fine punctations ; eyes flat. Coxa I has two short conical spurs, the external much longer than the internal. Hypostome with six rows of teeth. The marginal groove limits the festoons anteriorly. Capitulum long ; basis capituli short. Coxa IV with a spur nearly as long as the coxa. Length 3 mm. ; width 2·5 mm. (Neumann)

Female. Scutum triangular, nearly as broad as long, with a spot in the posterior angle ; eyes situated towards the anterior third of length of scutum. Coxa IV with a very short spur. Length 4·5 to 12 mm. ; width 3 to 8 mm. (Neumann)

This species is the common cattle tick of the United States, where it is known as the ' Lone Star Tick '; it also occurs in Guatemala, Guiana and Brazil.

Amblyomma hebraeum, Koch, C. L. **Male.** (Plate LXXIX, fig. 3) Scutum brown with yellowish markings and a transverse band not connected with the postero-median; longitudinal punctations very unequal, the largest situated on the band at the periphery. Eyes flat. Hypostome with six rows of teeth. Coxa I has two spurs, the internal flat and as broad as long, the external twice as long as the internal. Coxae II and III without spurs, coxa IV twice as long as broad, with one spur. Tarsi terminating abruptly at their extremities. Festoons, except the external ones, of a light colour. Length 5·6 mm.; width 4·8 mm. (Neumann)

Female. (Fig 4) Scutum triangular, almost as broad as long, and with a straight posterior angle; eyes towards the anterior fourth; numerous non-confluent punctations; a large medium patch extending to the posterior border of the scutum, with smaller lateral patches. Porose areas large, oval and parallel. Coxa IV with a short flat spur as broad as long. Length 6 to 20 mm.; width 5 to 13 mm. (Neumann)

This species is found in Cape Colony and German East Africa, chiefly on stock animals; it is also recorded from the giraffe, rhinoceros and many different kinds of antelopes. In South Africa it is popularly known as the ' Bont tick '. Neumann recognizes two varieties.

Variety *eburnum*, Gerst. Scutum of male with light yellow patches; the postero-median band joins the central transverse band, which is itself blended with the two parallel cervical bands. In the female the eyes are situated a little more anteriorly than in the case of *hebraeum;* the punctations are also finer. It is found in East Africa, and is parasitic on the lion, buffalo, different antelopes, the giraffe, and on a species of *Varanus.*

Variety *splendidum*, Giebel. Scutum of male without the transverse brown band; festoons, except the median and extreme ones, are light. In the female the punctations are finer, especially in the middle of the scutum. This variety is found on the buffalo and pig in East Africa and the Congo Free State.

Amblyomma variegatum, Fabr. **Male.** (Plate LXXIX, fig. 5) Scutum with large yellowish red marks; the brown transverse band in the centre separated by two large median clear markings: there is also a narrow longitudinal brown band which does not join the median transverse band. Eyes spherical. Punctations sometimes large and numerous, often very fine and unequal. Hypostome with six rows of teeth. Legs banded with yellow. Coxa I has two spurs, the internal flat and as broad as long, the external conical and twice as long as the internal.

Coxae II and III without spurs; sometimes the posterior border has a tuberosity. Coxa IV twice as long as broad, with a projecting spur. Tarsi not terminating abruptly. Festoons dark. Length 5 to 5·5 mm.; width 4·5 mm. (Neumann)

Female. (Fig. 6) Scutum triangular, nearly as broad as long, with a straight posterior border; eyes dark and situated towards the anterior fourth. Punctations numerous and large. Usually a well-marked light posterior spot on the scutum. Porose areas oval. Coxa IV with a spur as broad as long. Length 5 to 24 mm.; width 4 to 15 mm. (Neumann)

This species is found in Abyssinia, German East Africa, Zanzibar, Mozambique, Madagascar, Reunion, Mauritius, Angola, Congo, Guiana, Togo Land, Benin, Senegal, Guadelope, Guatemala, Ivory Coast and Antigua; it is parasitic on cattle, the horse, sheep, and sometimes on man.

Relation to Disease: Bionomics and Life Processes of Amblyomma hebraeum

As far as is known at present the life processes of the ticks of the genus *Amblyomma* are relatively simple; *Amblyomma hebraeum*, the ‘Bont tick’, the life history of which has been studied by Lounsbury, is a good example. This observer has carried out a long series of feeding experiments in connection with the transmission of the parasite of heartwater. He has shown that the infection does not pass through the egg of the tick, but that when it is ingested by the larvae it is transmitted by the nymph and possibly by the adult. The adult *hebraeum* almost always fixes itself on bare parts of the skin of its host; such places as the shoulders, the genitals and udders are favourite sites. The larvae and nymphs also prefer these parts to any others, but in the case of Angora goats they may be found attached among the long hairs on the sides and backs of the animals. The adult is never found on the backs of cattle, as it is apparently unable to climb through long hair. It always buries its mouth parts deeply into the skin, recalling the habits of the ‘Bont leg tick’, the popular name for *Hyalomma aegyptium*. Both the larvae and nymphs drop off when replete with blood, so that this tick, like most others of the genus whose habits are known, requires three hosts in order to complete its life processes. Its mating habits are peculiar, as the female searches for the male, which remains attached at one spot; this is quite unlike the habit of the other Ixodini, as the male usually moves about on the skin of the host and searches for the female. In the case of *hebraeum*, as Lounsbury points out, it is not uncommon to find one male surrounded by a dozen or more females each waiting to be fecundated. The male tick on finding a host at once attaches itself; the female wanders about until a male suitable for copulation is found; the male is not attractive until it has been on the host for at least five days.

GENUS APONOMMA, NEUMANN

Eyes absent. Capitulum long, basis capituli rectangular with humps on lateral borders. Second segment of palp without projections or humps externally. Body sub-circular, at least in the male. Scutum often marked with light spots. Spiracles usually triangular with rounded angles. Usually eleven festoons present, at least in the male. Coxa IV of male a little larger than the others. (Neumann)

Ticks of the genus *Aponomma* are characterized by the flat shape of their bodies, an adaptation to their habits, enabling them to pass under the scales of reptiles, which are their principal hosts. Almost every snake in tropical countries harbours one or more species of *Aponomma;* in Madras *A. gervaisi* is extremely common on the rat snake, *Zamenis mucocus.*

Neumann gives the following key to the species of *Aponomma.*

NEUMANN'S KEY TO THE SPECIES OF APONOMMA

MALES

1.	Scutum without marginal groove	2
	Scutum with marginal groove	8
2.	Body nearly as broad as long	3
	Body much broader than long	**tranversale.** (South Africa.)
3.	Scutum with numerous punctations	4
	Scutum smooth with a few superficial indistinct punctations	**laeve.** (Congo; German East Africa; Cape Colony.)
4.	Scutum with green or yellow markings	5
	Scutum without green or yellow markings	6
5.	Scutum with five green spots	**gervaisi.** (India; Burma; Ceylon; Java; Sumatra; Togo Land.)
	Scutum with nine green or yellowish spots	**exornatum.** (Natal; Transvaal; Senegal; Congo.)
6.	Tarsi II, III, and IV with a dorsal sub-terminal hump; scutum with deep punctations	7
	Tarsi with a dorsal hump; scutum light at the sides with superficial punctations	**ochraceum.** (German East Africa; Zanzibar.)
7.	Hypostome with eight rows of teeth; Coxa I with a spur as long as broad	**ecinctum.** (Philippine Islands.)

Hypostome with six rows of teeth ; coxa I with two very short equal spurs . . . **crassipes.** (Egypt.)

8. Hypostome with eight rows of teeth ; tarsi without sub-terminal humps ; scutum uniformly reddish brown . . . **trachysauri.** (Australia.)

Hypostome with six rows of teeth ; tarsi with sub-terminal humps . . . **9**

9. Scutum without deep marginal grooves, and with reddish spots. **decorosum.** (Australia ; Fiji Islands.)

Scutum with deep lateral grooves, brownish red without spots. **hydrosauri.** (Australia.)

FEMALES

1. Body as broad as long or longer than broad . . . **2**

Body much longer than broad . . . **transversale.**

2. Scutum with three green or yellowish spots . . . **3**

Scutum uniformly reddish brown, with green or yellow spots . . . **5**

3. Scutum much broader than long, with large punctations ; hypostome with six rows of teeth . . . **gervaisi.**

Scutum as long as broad or longer . . . **4**

4. Scutum with fine punctations ; hypostome with eight rows of teeth ; tarsi with spurs . . . **exornatum.**

Scutum with large punctations ; hypostome with eight rows of teeth ; tarsi without spurs . . . **trimaculatum.** (New Guinea.)

5. Scutum heart-shaped (lateral angles towards the anterior third) . . . **6**

Scutum triangular (the lateral angles towards the anterior fourth) . . . **8**

6. Hypostome with eight rows of teeth ; scutum with well marked punctations . . . **ecinctum.**

Hypostome with six rows of teeth ; scutum with very fine punctations . . . **7**

7. Tarsi long, without sub-terminal humps . . . **ochraceum.**

Tarsi short, with sub-terminal humps . . . **laeve.**

8. Scutum broader than long ; porose areas sub-triangular, and sub-contiguous . . . **trachysauri.**

Scutum as long as broad . . . **9**

9. Hypostome with six rows of teeth ; porose areas small, round, close, at a sub-tangent to the posterior border of basis capituli . . . **decorosum.**

Hypostome with eight rows of teeth ; porose areas large, oval and remote from each other . . . **hydrosauri.**

Aponomma gervaisi, Lucas. **Male.** Body as long or longer than broad. Scutum chestnut brown with five metallic green spots, one of which is median and the others at the periphery. Numerous deep unequal punctations. Hypostome with six rows of teeth. Coxa I has two spurs. Length 3 to 3·5 mm. ; width 2·5 to 3 mm. (Neumann)

Female. (Plate LXXII, fig. 6) Scutum heart-shaped, broader than long, with three green spots situated in the angles. Length 4 to 10 mm.; width 3·5 to 7 mm. (Neumann).

This species is found in most parts of India, Burma and Ceylon; it is also recorded from Java, Senegal, Luango and Togo Land; it is chiefly parasitic on snakes, but also occurs on lizards of the genus *Varanus*.

Genus Dermacentor, Koch, C.L.

Eyes flat. Capitulum short with rectangular base; palps short and thick; second segment not humped externally. Body nearly always much longer than broad. Scutum with light markings. Spiracles nearly always in the form of a short comma. The male as a rule has eleven festoons; anal groove present, but its limbs frequently do not join the genital groove. Coxa I has two well-developed spurs; coxa IV of the male is much larger than the other coxae. (Neumann)

Neumann gives the following key for the determination of the species.

Neumann's Key to the Species of Dermacentor

Males

1.	Scutum with light or dark marks.	2
	Scutum dark brown without marks	**nitens.** (United States; Guatemala; Venezuela.)
2.	Coxa IV with a single tuberosity on the posterior border	3
	Coxa IV with two or three small spurs on the posterior border	8
3.	Scutum with white spots	4
	Scutum with yellow or red markings (chiefly African).	7
4.	Second article of palp much broader than long, with a dorsal retrograde spine	**reticulatus.** (Europe; Persia; Japan; United States.)
	Second article of palp not broader or only a little broader than long, without a spine	5
5.	Spiracles with postero-external extension well marked.	**andersoni.** (United States; Montana.)
	Spiracles with less marked postero-external extension	6
6.	Spiracle smooth with very fine punctations	**variabilis.** (United States; Mexico.)
	Spiracle with prominent punctations	**variegatus.**
7.	Scutum with numerous markings resembling that of the female in front	**rhinocerotis.** (East Africa.)
	Scutum with eight peripheral spots	**circumguttatus.** (Congo; Cameroons.)

PLATE LXXX

Figure 1. Dorsal view of *Aponomma pattoni*, ♂. × 15.
Figure 2. Dorsal view of ♀ of same. × 12.
Figure 3. Dorsal view of *Dermacentor andersoni*, ♂. × 12.
Figure 4. Dorsal view of ♀ of same. × 12.
Figure 5. Dorsal view of *Dermacentor albipictus*, ♂. × 12.
Figure 6. Dorsal view of ♀ of same. × 10.

PLATE. LXXX.

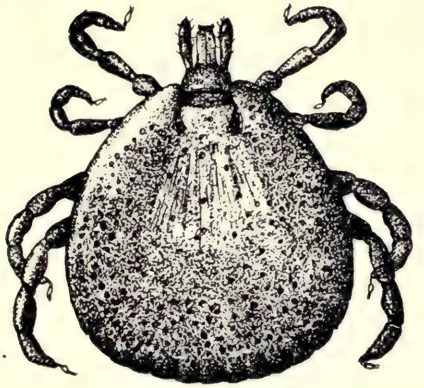
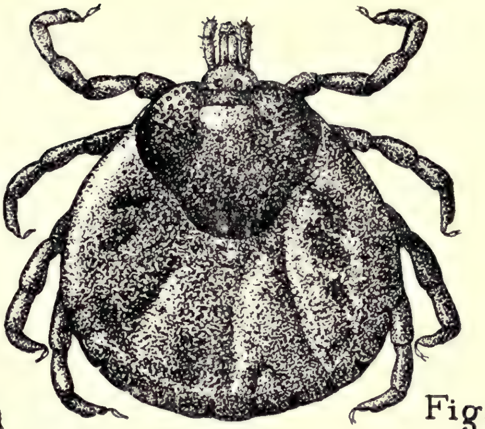


Fig. 1.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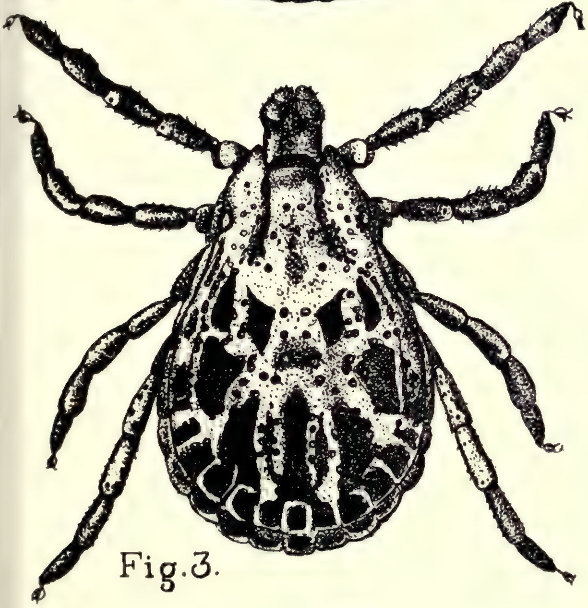
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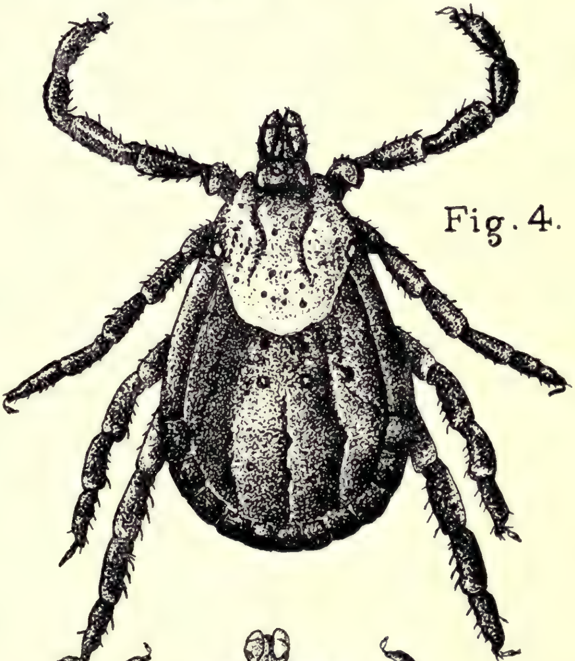
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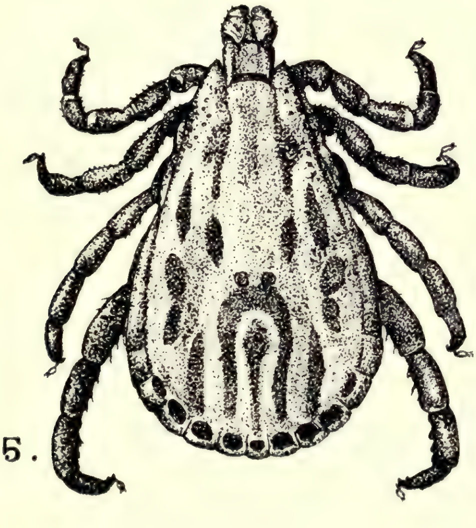


Fig. 5.

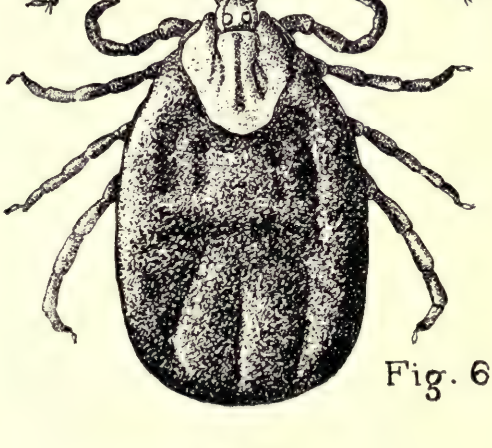


Fig. 6.

8.	Scutum white with blackish markings	**astrosignatus.** (Australia.)
	Scutum chestnut brown with or without white spots	**auratus.** (Burma ; Java ; Sumatra ; Borneo.)

FEMALES

1.	Scutum with light spots	2
	Scutum dark brown without spots	**nitens.**
2.	Scutum with white spots	3
	Scutum with yellow or red spots (chiefly African)	7
3.	Scutum longer than broad or as long as broad, without median hump	4
	Scutum broader than long with a longitudinal hump	**auratus.**
4.	Spiracle with ill-defined postero-external extension	5
	Spiracle with well-marked postero-external extension	**andersoni.**
5.	Scutum as long as broad	**reticulatus.**
	Scutum longer than broad	6
6.	Spiracle smooth with very fine punctations	**variabilis.**
	Spiracle with large well-marked punctations	**variegatus.**
7.	Scutum light on almost its whole surface	**rhinocerotis.**
	Scutum with three light spots, forming a triangle	**circumguttatus.**

Dermacentor reticulatus, Fabr. **Male.** Scutum chestnut brown with white markings and numerous deep unequal punctations; the lateral grooves not contouring the posterior border. Hypostome with six to eight rows of teeth. Palps as long as broad, the second segment with a small ventral retrograde spine. Coxa I has two contiguous well-developed spurs, the external one conical; a short spur on each of the other coxae. Coxa IV very large, much longer than broad; the spur towards the middle of its length. Length 5 mm.; width 3 mm. (Neumann)

Female. Scutum a little longer than broad; cervical groove long, no lateral grooves. Eyes situated about the middle of its length. Porose areas oval and directed towards each other. Length 5 to 16 mm.; width 2·5 to 10 mm. (Neumann)

This species is found throughout Europe; it is also recorded from the Caucasus, Turkistan, Persia, Siberia, Manchuria, Japan and Africa; it is parasitic on cattle, sheep, goats, deer, the pig, horse, hippopotamus, rhinoceros and several species of bats. Neumann recognizes two varieties, *niveus* and *occidentalis*.

Dermacentor andersoni, Stiles. **Male.** (Plate LXXX, fig. 3) Scutum chestnut brown with white spots sparsely scattered; punctations unequal; lateral groove uninterrupted and covered with punctations. Hypostome with six rows of teeth. Palpi much longer than broad, without dorsal retrograde spines. Coxa I with two long well developed contiguous spurs, the external conical; coxae II and III with two short spurs; coxa IV much longer than broad, with the spur at the antero-external angle, and one external spur. Spiracle with the postero-external extension well developed. Length 5 mm.; width 3 mm. (Neumann)

Female. (Plate LXXX, fig. 4) Scutum a little longer than broad; posterior border sinuous; eyes towards the middle of its length. Cervical grooves long and deep; lateral grooves wanting. Porose areas deep, diverging anteriorly and converging posteriorly. Length 5 to 12 mm.; width 3 to 8 mm. (Neumann)

This species is found in the United States, particularly in Montana; it is parasitic on horses and cattle, and often attacks man. It is the invertebrate host of the parasite (?) of Rocky Mountain Spotted Fever. According to Stiles it has been previously described under the name *Dermacentor occidentalis,* Marx; it is also spoken of as *Dermacentor venustus,* Marx.

Dermacentor variabilis, Say. **Male.** Scutum chestnut brown with white spots and deep sub-equal scattered punctations. Hypostome with six rows of teeth. Palpi longer than broad without dorsal retrograde spines. Coxa I has two well-developed contiguous spurs, the external conical; coxae II and III each have two short spurs. Coxa IV is a little longer than broad, and the spur is situated towards the posterior third. Length 5 mm.; width 2·5 mm. (Neumann)

Female. Scutum a little longer than broad with a concave border posterior to the eyes, which are situated about the middle of its length. Cervical grooves deep, united anteriorly with the lateral grooves, which are also deep. Porose areas deep and converging posteriorly. Length 5 to 14 mm.; width 2·5 to 9 mm. (Neumann)

This species is found in Mexico and the United States; it is parasitic on the cattle, the horse, hare, dog and lynx. Neumann recognizes one variety, *parumapertus.*

Relation to Disease

As already pointed out, *Dermacentor reticulatus* is believed to be the invertebrate host of *Piroplasma canis* in Europe, and it is also said to transmit *P. equi* in Russia. *Dermacentor andersoni,* Stiles, transmits the infective agent of Rocky Mountain Spotted Fever, a disease which affects man in the Bitter Root Valley in Montana, United States. The disease is not localized to Montana, but also occurs in Washington, Oregon, Idaho, California, Alaska, Nevada, Utah, Colorado and Wyoming.

Bishop and King, in a recent paper, give some data regarding the life processes of *Dermacentor andersoni.* The adult ticks, though present

Bionomics and Life Processes of Dermacentor

throughout the year, are most numerous during the months of April and May, when the weather is warm; with very rare exceptions it is only the adult stage which attacks man. Towards the end of summer the adults leave the plants on which they rest when waiting for a passing host, and crawl under the grass and leaves to hibernate; the larvae hibernate in the same manner. Bishop and King believe the mountain goat to be the reservoir of the parasite of Rocky Mountain Fever; infected ticks, chiefly larvae and nymphs, occur on the ground squirrel and the woodchuck, and these may carry the ticks from the higher altitudes to the valleys where cattle usually graze. In man the adults often fix themselves under the hair below the occipital region. In the Bitter Root Valley the life cycle of the tick extends over two to three years under natural conditions; the adults do not become replete with blood during the season in which they change to that stage.

Dermacentor andersoni, like most of the other species of the genus, requires three hosts in order to complete its life history; *variabilis*, the common dog tick in America, behaves in the same way. *Dermacentor nitens*, the American horse tick, and *D. nigrolineatus* and *D. albipictus*, do not leave their hosts until they become adults, the females dropping off when replete with blood.

GENUS HAEMAPHYSALIS, KOCH, C. L.

Eyes absent. Capitulum short with a rectangular base. Palpi short, the second segment generally humped externally. Body longer than broad. Scutum brown without spots. Spiracles circular or in the form of a short comma. Eleven festoons present, at least in the male; anal groove with limbs joining the genital grooves anteriorly. Coxa I has one spur and coxa IV of the male is a little longer than the others; trochanter usually with a retrograde spur at its distal extremity. (Neumann)

Neumann gives the following key for the determination of the species.

NEUMANN'S KEY TO THE SPECIES OF HAEMAPHYSALIS

MALES

1.	Second segment of palp without hump or with a hump on its external side and towards its posterior border	2
	Second segment of palp pointed externally at its posterior border	8
2.	Third segment of palp not recurved inwards	3

Third segment of palp prolonged in the middle line and recurved inwards . . . **concinna.**
(France; Germany; Austria.)

3. Coxa IV with a spur as long or nearly as long as the coxa . . . **punctata.**
(British Isles; Europe; Egypt; Algeria; Japan.)

Coxa IV either without a spur or with a short one . . . 4

4. Third segment of palp without spurs . . . **papuana.**
(New Guinea; Queensland.)

Third segment of palp with one or two retrograde spurs . . . 5

5. Scutum without lateral groove; third article of palp with a small spur on its posterior border . . . **birmaniae.**
(Burma; Sumatra; Borneo; China; Japan.)

Scutum with a lateral groove . . . 6

6. Coxae II, III and IV with one spur . . . 7

Coxae II, III and IV without spurs . . . **aculeata.**
(East Indies.)

7. Third segment of palp with unequal spurs; hypostome with ten to twelve rows of teeth . . . **neumanni.**
(Ceylon; Japan.)

Third segment of palp with sub-equal dorsal and ventral spurs; hypostome with eight rows of teeth . . . **parmata.**
(Cameroons.)

8. Palps much longer than broad, a little broader on their posterior than their anterior borders . . . **leporis.**
(United States; Mexico; Brazil; Argentine.)

Palps broader or nearly as broad as long, much broader on their posterior borders than on their anterior . . . 9

9. Second segment of palp not prolonged on the posterior border . . . 10

Second segment of palp with one or two retrograde humps on the posterior border . . . 14

10. Coxa IV with a short spur . . . 11

Coxa IV with a very long spur . . . 13

11. Scutum without a lateral groove . . . **simplex.**
(Madagascar.)

Scutum with a lateral groove . . . 12

12. Scutum with very fine scattered punctations, nearly obsolete . **flava.**
(South India; Ceylon; Japan.)

Scutum with very visible punctations close together . . . **numidiana.**
(Algeria.)

13. Coxa IV with a simple spur; third article of palp with one ventral spur . . . **flava armata.**
(Japan.)

Coxa IV with two contiguous spurs, the external the shorter; third article of the palp with one ventral and one external spur . . . **cornigera.**
(Borneo; Sumatra; Java.)

14. Coxa IV with a spur as long as the coxa . . . 15

Coxa IV with a short spur . . . 16

15. Scutum as long as the body; hypostome with ten rows of teeth . . . **spinigera.**
(India, West Coast; Ceylon.)

Scutum not as long as the body; hypostome with six rows of teeth . . . . **elongata.**
(Madagascar.)

16. Second segment of palp with one spur on the postero-ventral border; hypostome with eight rows of teeth . . . . **calcarata.**
(Abyssinia.)

Second segment of palp with one spur on its posterior border; hypostome with ten rows of teeth . . . . **leachi.**
(Egypt; Abyssinia; Transvaal; Congo; Togo Land; Sumatra.)

FEMALES

1. Second segment of palp without a hump, or humped on its external surface towards its posterior third 2
Second segment of palp pointed externally on its posterior border 8
2. Third segment of palp with a ventral retrograde spur 3
Third segment of palp without ventral retrograde spur 7
3. Third segment of palp without a retrograde dorsal spur 4
Third segment of palp with a dorsal retrograde spur 5
4. Second segment of palp rounded externally; coxae I and IV with equal spurs . . . . **punctata.**
Second segment of palp angular externally; coxae I with a long spur, and coxa IV with a very short spur . . . . . **concinna.**
5. Coxa I with a spur as long as the ventral spur of the third palpal article 6
Coxa I with a short spur . . . . **parmata.**
6. Scutum circular . . . . **birmaniae.**
Scutum a little angular and contracted posteriorly . . . . **neumanni.**
7. Second segment of palp angular externally; hypostome with ten rows of teeth . . . . **papuana.**
Second segment of palp not humped externally; hypostome with six rows of teeth . . . . **ambigua.**
(Japan.)
8. Palps much longer than broad, a little broader on their posterior than on their anterior borders 9
Palps broader or as broad as long, much broader on their posterior borders 16
9. Third segment of palp with an obsolete spur; coxa I with a poorly developed spur . . . . **leporis.**
Third segment of palp with a well developed ventral spur; coxa I has a broad strong spur . . . . **flava.**
10. Second segments of palps without hump on its posterior border 11
Second segments of palps with one or two retrograde humps on their posterior borders 12
11. Scutum oval, longer than broad . . . . **numidiana.**
Scutum as broad as long, discoidal . . . . **cornigera.**
12. Second segments of palps with a retrograde hump 13
Second segments of palps with a dorsal and ventral hump 14

13.	Second segments of palps with a long ventral hump ; hypostome with ten rows of teeth	**spinigera.**
	Second segments of palps with a short ventral hump ; hypostome with six rows of teeth	**elongata.**
14.	Scutum oval, longer than broad ; second segment of palps with strong spurs	**leachi.**
	Scutum discoidal ; second segment of palps with poorly developed spurs	**spinulosa.**

Haemaphysalis concinna, Koch, C.L. **Male.** (Plate LXXXI, fig. 1.) Palps much longer than broad, second segment angular towards its posterior third ; third segment shorter than the second, with a short retrograde ventral spur, and prolonged towards the middle line, curving inwards. Basis capituli with prominent posterior angles. Scutum with numerous fine equal punctations. Coxa I has a spur at least twice as long as broad ; coxae II, III and IV with short spurs. Tarsi long and slender. Hypostome with twelve rows of teeth. Length 3 mm. ; width 1·7 mm. (Neumann)

Female. (fig. 2) Scutum discoidal. Porose areas short and oval. Hypostome with ten rows of teeth. Length 3·2 to 5·5 mm. ; width 2 to 3 mm. (Neumann)

This species is found in France, Germany, Austria and Poland ; it is parasitic on sheep and deer.

Haemaphysalis birmaniae, Supino. **Male.** Palps a little longer than broad ; second segment angular externally near its posterior third ; third segment shorter than the second and provided with a small spine on its postero-dorsal border, and another, nearly as long as broad, on the ventral border. Hypostome with ten rows of teeth. Basis capituli with posterior angles developed into projecting points. Scutum with numerous equal fine punctations. Coxa I with a spur at least twice as long as broad ; coxae II, III and IV each with one spur broader than long. Length 2·7 mm. ; width 2 mm. (Neumann)

Female. Scutum sub-circular. Porose areas oval, parallel, deep and very short ; other characters the same as in the male. Length 3·5 to 5·5 mm. ; width 2·3 to 4 mm. (Neumann)

This species is found in Burma, India, China, Japan, Sumatra and Borneo ; it is parasitic on the horse, cat, bear and goat.

Haemaphysalis punctata, Can. and Fan. **Male.** Palps with the second segment rounded externally, without a retrograde spine ; third segment as long as the second and with a ventral retrograde spine. Hypostome with ten rows of teeth. Basis capituli with slightly prominent posterior angles. Scutum with numerous equal punctations. Coxae I

PLATE LXXXI

Figure 1. Ventral view of *Haemaphysalis concinna*, ♂. × 16.
Figure 2. Dorsal view of ♀ of same. × 16.
Figure 3. Ventral view of *Haemaphysalis leachi*, ♂. × 18.
Figure 4. Dorsal view of ♀ of same. × 18.
Figure 5. Ventral view of *Haemaphysalis bispinosa*, ♂. × 20.
Figure 6. Dorsal view of ♀ of same. × 20.

PLATE. LXXXI.

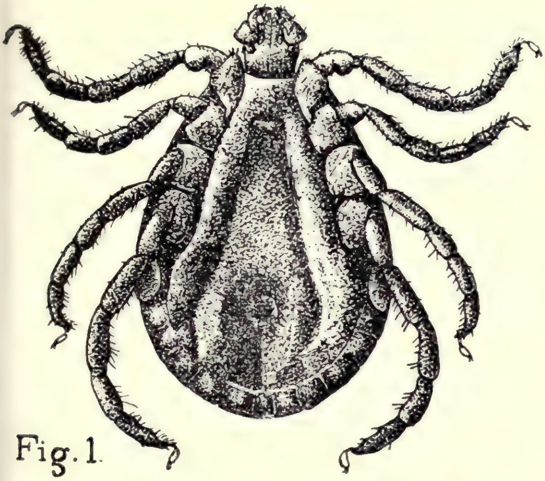
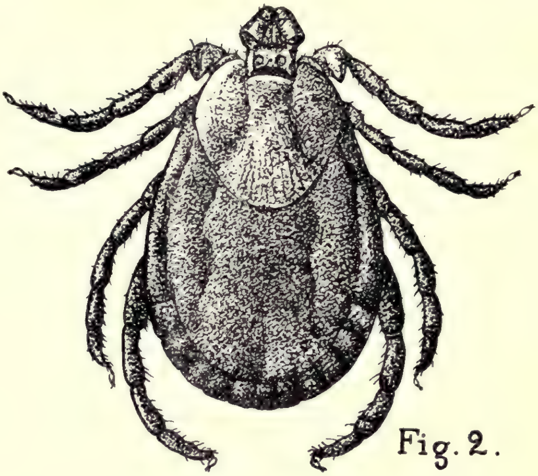


Fig. 1.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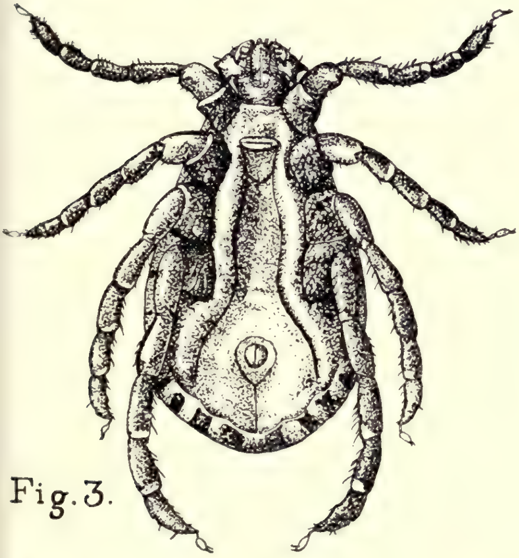
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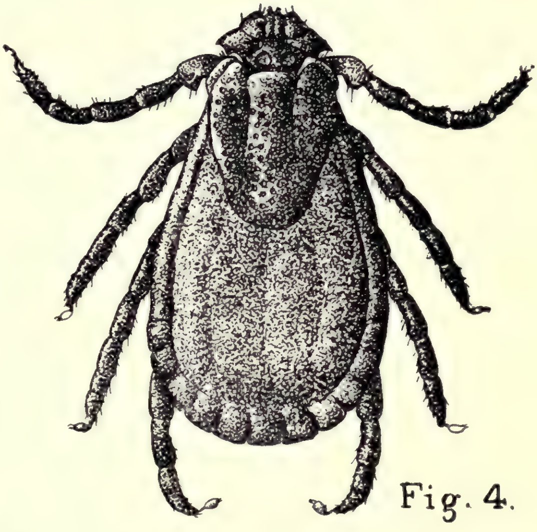
Fig. 4.

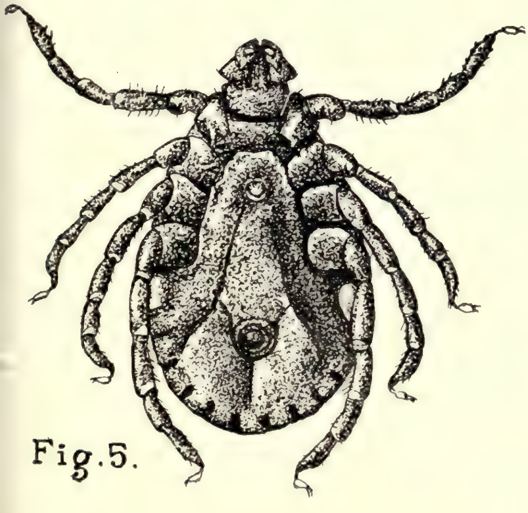
Fig. 5.

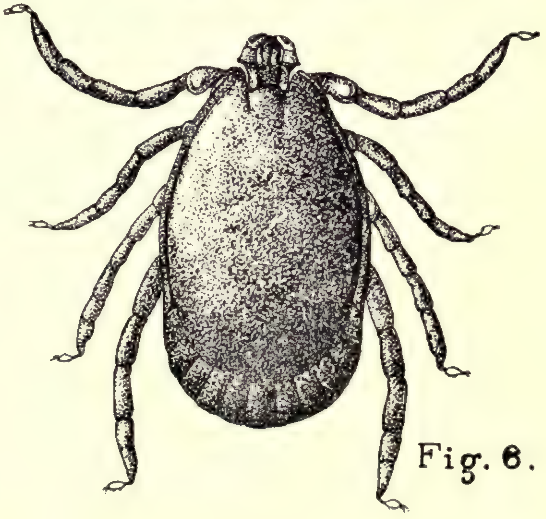
Fig. 6.

II and III each with a short spur ; coxa IV with a spur as long or longer than the coxa. Tarsus IV short, nearly three times as long as broad. Length 4 mm. ; width 2 mm.

Female. Scutum oval ; longer than broad. Cervical grooves long and superficial ; porose areas large and sub-circular, but not very well marked. Coxa IV with a spur as long as coxa I and longer than those of coxae II and III. Length 3·5 to 12 mm. ; width 2 to 7·5 mm.

The species is found in the British Isles, France, Germany, Holland, Italy, Roumania, Crete, Dalmatia, Greece, Algeria, Egypt, the Canary Islands and Japan ; it is parasitic on cattle, the goat, sheep, deer and horse. As already noted it has been proved to be the invertebrate host of *Piroplasm bigeminum* in England.

Bionomics and Life Processes of Haemaphysalis

Ticks of the genus *Haemaphysalis* are sluggish and feeble in their movements, and are difficult to experiment with. As far as is definitely known they require three hosts in order to complete their life histories. As a rule they attach themselves about the ears and faces of their hosts, but some select the scrotum and udder ; they are very easily dislodged. Many of the common species do not appear to select any particular host, but will fix themselves to a number of different animals.

SUBFAMILY SPELAEORHYNCHINAE

Body broad and flat, with scutum in the female, and a ventral chitinous plate behind the capitulum. Genital plate absent. Anus sub-terminal. Genital opening situated just anterior to the anus. Spiracles small and situated just external to the third intercoxal space. Capitulum terminal ; epistoma semi-dome-shaped, hollowed out ventrally ; it encloses the hypostome and mandibles. The former is styliform and unarmed ; the latter are well developed and end in two hooks ; the maxillae are separate, small, and membraneous. The palps are slender and are five jointed. Legs without spurs. (Neumann)

Neumann recognizes one genus, which contains the single species *praecursor*, of which the male is unknown. The female was found in Pernambuco on the bat *Carollia brevicaudus.*

TABLE OF GENERA OF IXODIDAE

IXODINI	GROUP I.	Anal Groove contouring anus anteriorly.	Palps of both sexes hollowed out	**Ixodes.**
			Palps pyriform, not hollowed out in the male; legs very long	**Eschatocephalus.**
			Palps not hollowed out; third segment conical in male	**Ceratixodes.**
	GROUP II.	Anal Groove contouring anus posteriorly.	Capitulum short; eyes present; male without true anal plates; coxa IV very large	**Dermacentor.**
			Capitulum short; eyes present; male with anal plates; spiracle comma-shaped	**Rhipicephalus.**
			Capitulum short; eyes present; male with anal plates; spiracle circular; anal groove obsolete	**Margaropus.**
			Capitulum long; eyes prominent; male with anal plates	**Hyalomma.**
			Capitulum long; eyes flat; male without true ventral plates; scutum ornate	**Amblyomma.**
			Capitulum short; eyes absent	**Haemaphysalis.**
			Capitulum long; eyes absent; body broad and flat	**Aponomma.**
ARGATINI			Body flattened; margin without mammillae, but with discs	**Argas.**
			Body without flattened margin, but with mammillae	**Ornithodorus.**

Salient points in the identification of Ticks

To identify any species of tick the worker must first be able to recognize the genus to which it belongs, and it may be of help before leaving the subject to emphasize some of the points which are important in this connection; it is not necessary however, that the worker should be able to name the tick with which he is experimenting, provided that he is able to place it in its proper genus and to be certain that he is dealing with one species only; the species can be determined later by an expert. When examining a specimen it is first necessary to decide whether it is an adult or not; the immature stages of *Argas* and *Ornithodorus*, for example, closely resemble the adults, more particularly the males, but they can be distinguished from them at once by noting the condition of the genital opening, which is entirely absent in the young stages, but patent in the adults. In the subfamily Ixodinae all the females have porose areas on the dorsal surface of the capitulum, and if these are absent the specimen is either a male or a nymph.

The genera of the Ixodini are apt to cause some confusion. It will be seen from the table on page 632 that they fall into two main groups, according as to whether the anal groove contours the anus in front or behind; in the case of many replete females it may not be very apparent, and in this case it is best to examine an unfed tick. Of the three genera included in the first group, *Eschatocephalus* and *Ceratixodes* contain only somewhat rare species, and need not be considered further; the characters mentioned on page 590 will serve to define the genus *Ixodes*.

If the anal groove contours the anus posteriorly the tick may belong to one of seven genera. The capitulum provides the next determining character. If it is relatively short in proportion to the rest of the body, the specimen belongs to one of four genera, *Dermacentor*, *Rhipicephalus*, *Margaropus* or *Haemaphysalis*; if it is long, to one of three, *Hyalomma*, *Amblyomma* or *Aponomma*. Of the first group of four, *Dermacentor* is distinguished by the rectangular shape of the basis capituli, by having the second segment of the palp about as broad as long, by the ornamented scutum, and by the presence of eyes, and if the specimen is a male coxa IV will be larger than the others, though this is not a reliable character. In *Rhipicephalus* and *Margaropus* the basis capituli is rectangular, and has projecting sides; in the former the palps have no transverse ridges, and the spiracle is as a rule comma-shaped, while in the latter there are short ridges on the second and third segments of the palps, and the spiracle is circular or nearly so in both sexes.*

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* It should be remembered that the shape of the spiracle may differ in the two sexes.

Haemaphysalis is distinguished from the other genera by having the base of the second segment of the palp, always wider than the basis capituli, and by the absence of eyes. Of the second group of three genera, *Hyalomma* and *Amblyomma* are not easy to separate from one another; in the former the eyes are button-shaped, at least in *Hyalomma aegyptium*, and project from the pits in which they lie in a very characteristic manner in both sexes, and the second and third segments of the palps are about the same length. In *Amblyomma* the eyes are flatter and do not project to any marked extent, and the second segment of the palp is longer than the third. The species of *Aponomma*, which are mainly parasitic on reptiles, have broad flat bodies, and are always without eyes.

BREEDING AND MANIPULATION OF TICKS FOR EXPERIMENTAL PURPOSES

Success in the breeding and manipulation of ticks depends to a large extent on an accurate knowledge of their life histories, the habits of the early stages, and on the methods suitable for keeping their hosts in captivity. When these are known the technique in most cases is simple, and all the apparatus which is necessary is easily obtained.

In view of the great variations which are found in the life histories of the ticks of the different genera, it will be convenient to consider each genus separately, and in doing so to recapitulate briefly the main features of the life cycles in their relations to the technique which has to be adopted to meet the case. The types of life cycles which are found in each genus have been indicated in the foregoing descriptions. The life history of every tick consists of four stages, the egg, the larva (characterized by the possession of six legs), the nymph and the adult, male or female; there is in reality also a fifth stage, for the adults are not functionally mature for a varying period after their emergence from the nymphal stage. The nymph can always be distinguished from the adult by the fact that the genital opening is not patent. All these stages are as a rule blood-suckers; there are however, a few exceptions as already noted.

The variations which exist in the life cycles depend upon the relations of the several stages to the host, and it is evident that a great variety of types is conceivable. The entire life from egg to adult may be completed on one species of animal as host, or the succeeding stages may feed on other species. The early stages may remain attached to the host while they pass through the metamorphosis, or they may drop off when replete with blood, remaining concealed apart from the host until they have digested the meal and passed on to the next stage; only one feed may be taken, or several, and in many of the Argatini the female may feed more than once between each act of oviposition. Copulation usually takes place on the skin of the host, the smaller and more active male seeking out the female, though in rare cases, such as that of *Amblyomma hebraeum*, the female searches for the male. The proportion of the life of the adult stages which is passed on the skin of the host varies considerably; in most of the genera of the Ixodini the females fill up with blood in a comparatively short time, but in *Aponomma* they may remain attached to the host for a long period, often extending to months. It must not therefore be supposed that all ticks which are firmly attached to their host are in the act of feeding, for this is not necessarily the case; they may remain attached for a considerable time without any appreciable increase in size, and then become distended in an hour or so; this is commonly seen in the case of *Aponomma gervaisi*.

The types of life history which are met with may be conveniently grouped into four classes as follows:—

CLASS 1. Ticks the larvae of which feed on one species of animal, or on a group of related animals; the adults, and to a certain extent the nymphs also, may feed on many different kinds of animals but as a rule not on the species which serves as host for the larva; both the larvae and nymphs always drop off to undergo the metamorphosis, after which they become attached to another individual. *Hyalomma aegyptium* is a good example of this type; its larvae will only attach themselves to some small mammal, never to the species of host on which the adults are found. According to Dönitz the larvae may feed on some particular bird or group of birds (hawks). *Rhipicephalus simus* and *R. capensis*, as shown by Lounsbury's experiments, also conform to this type, for though the adults and nymphs are found on most farm animals the larvae will not feed on them.

CLASS 2. Ticks the larvae, nymphs and adults of which feed either on one particular group of animals (Reptilia, Leporidae, etc.), or indiscriminately on a great variety of animals. The majority of ticks belong to this class. The first type is exemplified by the ticks of the genus *Aponomma* and by some species of *Haemaphysalis*. *A. gervaisi* for instance occurs in all its stages on many species of snakes and lizards, but has never been taken from a mammal. *Haemaphysalis leporis* has adapted itself to the habits of the Leporidae and is rarely found on other hosts. *Haemaphysalis bispinosa* is a good example of the second and commonest type; it has been found in all its stages on most of the common mammals in Madras, but never on reptiles. In this class both the larvae and nymphs always drop off to moult.

CLASS 3. Ticks the larvae, nymphs and adults of which feed on different animals of the same or another species, but undergo the first moult on the host, while the nymph always drops off when replete with blood. The larval and nymphal stages are therefore passed on one individual, the adult stage on another of the same species or a different one. As far as is known at present, *Ornithodorus megnini*, *Rhipicephalus bursa* and *R. evertsi* are the only ticks which belong to this class. *Ornithodorus megnini* is of special interest, since the adult, like that of the Oestridae in the Diptera, does not feed, reproduction being carried out on the food material accumulated in the early stages.

CLASS 4. Ticks which in all their stages feed on one particular species of animal or its near allies; the larvae and nymphs always moult on the host. To this group belong the species *Margaropus annulatus* with its varieties, *Dermacentor nitens*, *D. nigrolineatus* and *D. albipictus*.

The degree of association between ticks in their several stages and the host presents an interesting and somewhat perplexing problem in parasitology, all the more interesting because it is full of practical importance. The simplest life history would appear to be one in which a tick in any of its stages could adapt itself to any host, and thus ensure the continuity of its species; the most advanced is probably to be found in the fourth class, in which the larvae and nymphs moult on the host. In view of the fact that the Ixodini as a rule leave their hosts to moult in their larval and nymphal stages, large numbers must necessarily fail to find a host and die; this great disadvantage is probably overcome by the very large number of eggs laid by these ticks; in the case of *Hyalomma aegyptium*, for instance, the number may run to many thousands. The Argatini, as Nuttall has pointed out, are ticks of the habitat and the difficulties of finding a host are very much minimized, and as a result their progeny is proportionately smaller. The worker interested in this subject should consult Nuttall's paper on the 'Adaption of Ticks to the Habits of their Hosts'.

The practical interest of the subject lies in the transmission of parasites by means of ticks from one vertebrate to another. The chances of transmission are evidently greatest in those cases in which each stage feeds on a different individual, dropping off to moult, and least when the cycle from larva to adult is passed on the same animal. Parasites ingested by one stage may be transmitted to another host when the next stage becomes attached to it, or by the next but one; in those cases in which the larvae and nymphs are restricted to one animal, the parasite can only be transmitted by the larvae when they first become attached, and here the problem is complicated by the occurrence of hereditary infection. The larvae hatching out of eggs laid by an infected female are capable of passing on the infection to the host in one or other of the stages of the second generation.

In the following account of the technique employed in breeding and experimenting with ticks the genera will be considered separately, in order to show the modifications which the special circumstances require in each case.

Argatini: Genus Argas

Ticks of the genus *Argas* are somewhat peculiar in their feeding habits. The larva as far as is known is a blood-sucker, and always remains attached to its host for several days; shortly before it drops off it assumes the characteristic flat shape of body, which, as already pointed out, is a special protective adaptation, since a flat tick can more easily pass into a narrow slit than one which is swollen dorso-ventrally. The first nymph is a rapid feeder and takes from twenty minutes to half an hour to take a full meal of blood; it then detaches itself and crawls away to hide in the abode of its host. The second and only other nymphal instar behaves in the same way. The female takes a feed of blood and after a short period becomes sexually mature; the male may or may not feed before copulation, which always takes place in the resting place. After another period the females begins to oviposit, laying the eggs in batches of 100 or more and usually returning to the host to take a feed between each act of oviposition. The larvae hatch out in about ten days, and the life history begins again.

The nymphs and adults of most of the species of *Argas* are nocturnal in their habits, behaving exactly like the bed bug. Some, owing to the habits of their hosts, are diurnal feeders. *Argas vespertilionis*, which is parasitic on a number of bats in Madras, but more particularly on *Scotophilus kuhli*, the yellow bat, has been taken in all its stages from its host when caught in its resting places during the day.

Argas persicus: Breeding technique

For breeding and experimenting with *Argas persicus*, the fowl tick, a cage suitable for imprisoning the host is required. One similar to that shown on Plate LXXXII, fig. 1, is very convenient, and will also serve for a variety of purposes. The cage measures one foot in each dimension, and consists of a number of iron rods rivetted to an iron framework; a wire frame (not shown in the photograph) rests on a ledge on the inside, and serves as a foot rest when one is required; underneath this there is a tray or underpan made of galvanized iron, to catch the urine or faeces when the cage is used for a small animal. Such cages are inexpensive, and have the great advantage that they can be sterilized by immersing them in boiling water, to kill off eggs, larvae, etc., which may be in the crevices and would interfere with experiments. They can be painted to prevent the metal rusting. These cages, with larger ones of the same pattern, were devised by Major Christophers for dogs used in experiments with ticks and *Piroplasma canis.*

For experiments with *Argas persicus*, the wire foot rest and underpan are removed, and the cage is placed in a strong white cloth bag, made to fit it and fastened at the top with a running tape. The head of the fowl is enclosed in a muslin bag secured with a purse string, the tapes being crossed and tied under the wings, to prevent it from eating the ticks, of which most fowls are very fond. The larvae are dropped either on some clean straw placed in a corner of the cage, or placed under the wing of the fowl. The bird is then placed inside the cage, which should be protected from ants by placing it on a table the legs of which are standing in antiformicas. Only a moderate number of ticks should be placed in each cage, or they will kill the host from loss of blood. If the experiment is allowed to go on indefinitely through several generations of ticks the cage will literally swarm with them.

At least once a day the host is removed from the cage and given food and water, care being taken that it does not rid itself of its parasites while it is at liberty, which it will certainly attempt to do if it is not watched. The larvae drop off when full-fed, and collect in the crevices of the framework of the cage. When all the larvae have left the host the latter should be removed, and the bag changed. As soon as the first nymphs appear, as will be readily seen by examining the cage, the fowl is replaced for two successive nights and after this at intervals of a week or ten days.

Argas vespertilionis: Breeding technique

In order to experiment with *Argas vespertilionis* it is necessary to obtain one of the several species of bat on which it feeds, and to devise some method of keeping it in captivity for a considerable time. The roosting places of *Scotophilus kuhli*—one of the hosts of this tick in Madras—are holes in banyan trees; on locating one, a large butterfly net is held over the outlet about the time the bats are accustomed to come out in the evening; the bats fall into it as they fly out. They should be caught and transferred to small cloth bags, which are securely fastened with a purse string and then hung up in a dark place; the cloth of which the bag is made should be strong or the bat may bite a hole through it and escape. The larvae of *A. vespertilionis*, which are always attached to the wing membrane, drop off during the day; they should be collected and placed on crumpled filter paper in a small specimen tube, which is then kept in the dark. The bat must be fed on milk, which it will readily suck up from a piece of cotton wool. After all the larvae have dropped off the bat may be liberated, as it will not survive long enough in captivity to be of further use, and others can be obtained from the same resting place. The nymphs and adults may be fed by placing them in the bag with the bat.

Genus Ornithodorus: O. savignyi

Ornithodorus savignyi and *O. moubata* are much alike in their feeding habits; their larvae never suck blood, but remain in a dormant condition until the first moult takes place. In captivity both species will feed on almost any animal. A number of males and females having been procured they should be placed in a large earthenware tray containing some fine sand, in which they soon bury themselves. It is useful to know that both *savignyi* and *moubata* travel well by post if they are placed with some sand in a small tin, the lid of which is perforated with small holes. All the stages can be easily fed on calves. A small area of the skin on one flank is shaved and the animal thrown on the ground and held firmly down; the ticks are then picked up between the fingers and placed on the skin. If they are ready to feed they will do so in a short time, filling up with blood in from fifteen to thirty minutes. It will be noticed that they become surrounded by a clear fluid, which comes from their Malpighian tubes and coxal glands. It is believed that ticks infected with spirochaetes contaminate the wound with some stage of the organism which lives in the excretion of the Malpighian tubes; this, however, is doubtful, and more recent observations tend to show that this is not the route by which the spirochaete gains access to its vertebrate host. If a calf is not available the ticks can be just as easily fed on a dog, rabbit or a guinea pig; they seem to thrive on the blood of any of these animals.

Ornithodorus moubata

Moubata is a domestic tick, and it may be collected in large numbers from the dust from the floors of native huts in those parts of Africa and Madagascar where it is prevalent; it is commonly found in the bed mats used by the natives and may in this way be carried long distances to fresh localities. It can be reared with great ease by adopting the methods recommended in the case of *savignyi*.

All the other species of *Ornithodorus*—except *O. megnini*—the habits of which have been observed appear to have the same life history as *savignyi* and *moubata*, each passing through four nymphal stages before becoming adults. *O. megnini* is very peculiar in its feeding habits.

Ornithodorus megnini

The 'Spinose ear tick'—the popular name of *megnini* in the United States—is chiefly found on the horse, occasionally on cattle; sometimes it attacks man. As its name implies, it attaches itself to the ear, often passing inside and burying itself deeply in the skin. Hooker has studied its habits. He placed the larvae in cloth bags (see page 644) which were fixed over the ears of cattle. The larvae soon buried themselves deep down in the folds of skin. About five days later, and while still attached, they shed their skins and became nymphs; these remained on the cattle for several months, during which time they slowly became replete. They then detached themselves, and on dropping to the ground (the bags being removed) crawled up the wall or wooden posts in the pen and hid in cracks and crevices several feet above the ground; after about a week the final metamorphosis took place. This stage, according to Hooker, does not feed; unlike all the other species of *Ornithodorus* the habits of which are known, the female *megnini* lays all her eggs in one batch and dies. It should be noted that *megnini* has only one nymphal stage.

Genus Ixodes

The life histories and habits of ticks of the genus *Ixodes* (including the subgenera *Eschatocephalus* and *Ceratixodes*) are typical of the family Ixodidae. As far as is known all the species require three hosts, which may belong to the same or to different species. As regards their habits these ticks come nearest to the Argatini. Nuttall, in his valuable papers on the subject, points out that a large number of the males of *Ixodes* are unknown, and that this is mainly due to the fact that they are never found attached to the vertebrate host, but remain in their burrows or nests, where they seek the females for copulation. In this habit these ticks recall some of the species of the genus *Argas*, for instance, as *Argas vespertilionis* and *Argas brumpti*. On the other hand the males of many *Ixodes*, like most Ixodinae, are to be found with the females on the host.

Nuttall has recently recorded some valuable observations on the life processes of several species of *Ixodes*; as these observations have a direct bearing on the carrying out of laboratory experiments necessitating the manipulation of the ticks they are here summarized. It should, however, be remembered, as Nuttall himself points out, that the data obtained from the study of the life processes of ticks in the laboratory, where they are kept apart from their true hosts and natural surroundings, are to a certain extent fallacious, the conditions being unusually favourable; this, however, in no way detracts from their value as a guide to the worker.

Ceratixodes putus

Ceratixodes putus is parasitic on birds, and Nuttall found large numbers in the nests of guillemonts in South Wales. The nests consist of hollows in caverns in precipitous cliffs and can only be reached from the brow of the cliff with the assistance of a rope. All the other stages except the unfed larvae were found in the damp earth of the nest; numbers of the unfed females were encountered on the exposed rocks. Nuttall made numerous attempts to feed the larvae, nymphs and unfed females on fowls, ducks and gulls, but without success. It would appear that the ticks were placed on the birds, the bare skin under the wing being the part selected; it has often been noted by the senior author that ticks which are placed directly on a host take much longer to attach themselves than if they are placed in a cage with a host or in a bag or cloth close to its body, and in some cases fail to do so. The failure noted above may have to do with some particular site at which the tick feeds. Nuttall's observations have, however, demonstrated that *C. putus* requires three hosts, and that the male never sucks blood, but after emerging from the nymphal stage waits for the replete female, with which it immediately copulates; all the stages may live for long periods without food.

Ixodes ricinus

Ixodes ricinus, the common cattle tick of Europe, has been bred by Nuttall on cattle and rams. The larva remains attached from 4 to 10 days on the calf; the nymph 3 to 6 days on a ram and the adults 4 to 7 days on the same host. The period which elapsed before the eggs hatched was from 49 to 62 days and from larva to nymph 124 days. Oviposition began from 17 to 24 days after the females were full-fed and lasted from 32 to 45 days, the female laying from 2,400 to 3,200 eggs. Females may survive ten days after oviposition is complete. It is comparatively easy to manipulate this tick once the larvae have been obtained. As the methods likely to be employed are similar to those adopted in the case of other ticks of cattle they will be dealt with fully further on. The manipulation of *Ixodes ricinus*, for instance, would be very similar to that of *Rhipicephalus appendiculatus* and *R. simus*. *Ixodes hexagonus* may be handled in the same way as *Rhipicephalus sanguineus* and *Haemaphysalis leachi*. Hadwen has successively raised *Ixodes angustus* on the squirrel, *Scuirus hudsonius* *douglasi,* and the hare, *Lepus dalli.* The best methods of keeping these animals in captivity are noted further on in connection with experiments with *Haemaphysalis.*

Genera Rhipicephalus and Margaropus: R. sanguineus, the dog tick

Experiments with *Rhipicephalus sanguineus* may be carried out on the dog; young pups just able to lap milk should be used, as they are easily handled. As already pointed out the dog tick requires three hosts, either of the same or of different species, to complete its life history. The larva remains on the dog from 5 to 8 days, the nymph from 5 to 7 days and the adults from 8 to 10 days; oviposition begins 2 to 4 days after the female drops off and is completed in about a week. The larvae hatch out in from 7 to 10 days and are ready to feed in from 2 to 3 days. The cage (Plate LXXXII, fig. 3) suitable for experiments with this tick is similar to the small one described above; it measures 2 ft. × 15½ in. × 16 in. If the worker wishes to experiment with *Piroplasma canis,* a pup should be obtained and isolated for about a week in a cage until all the ticks it harbours have dropped off; they can be collected by placing the cage in a large cloth bag as shown in the figure on the plate. The males should be picked off with a pair of forceps and destroyed; it is important to examine the insides of the ears, for this tick prefers this situation to any other, and may very easily be overlooked. If the dog is free from infection it should be transferred to another cage which has been dipped in boiling water. The ticks for the experiment may now be liberated in the cage, first taking care to remove the underpan, otherwise some of the ticks may drop into the urine which collects in it and will be drowned; the wire foot-rest is left in the cage for the animal to stand on. The method of liberating the ticks is as follows:—Some straw is dipped in boiling water to kill off stray ticks, and dried in the sun; it is then placed in the cage near the animal and the ticks are dropped on to it. This method of placing the ticks has many advantages over any other. It imitates natural conditions, for ticks are accustomed to crawl up blades of grass, sticks, etc., and to wait for a passing animal; they crawl about on the straw in the cage, and when the dog touches it they transfer themselves to its body and soon become attached. If ticks are dropped on to the body of the dog, they begin crawling about, which irritates the animal and causes it to attempt to dislodge them; they may fall through the meshes of the foot-rest on to the cloth below, and a long time may elapse before they find their way back again. In using straw there is the further advantage that there is no necessity to wait until each tick becomes attached, as must be done

PLATE LXXXII

Figure 1. Small iron cage suitable for experiments with *Argas persicus*. The cage is standing on a table partly surrounded by a cloth bag. A fowl with a head bag is seen at the side.

Figure 2. Calf box made of old deal-wood cases; suitable for experiments with cattle ticks. A calf with an iron neck collar is seen standing in the box.

Figure 3. Large iron cage similar to that shown in fig. 1. This cage is suitable for experiments with dog ticks.

Figure 4. Goat dressed in a cloth garment; the right ear is also enclosed in an ear bag (see page 646).

Figure 5. A calf with belly bag (see page 645).

Figure 6. Cage suitable for experiments with wild animals such as the jackal (see page 643). The foot-board is seen half way up, and it is between it and the upper bars that the animal is secured.

Figure 7. Wire cage for experiments with snake ticks (see page 650).

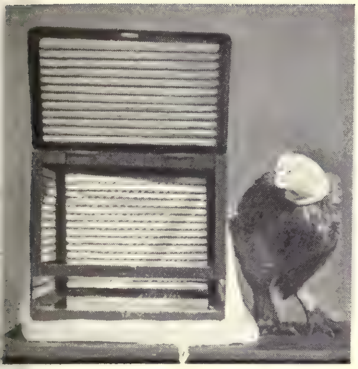


Fig. 1.

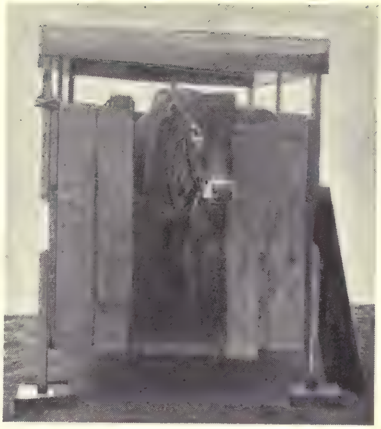


Fig. 2.

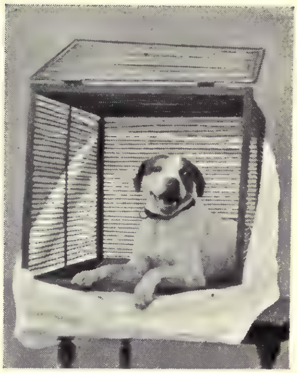


Fig. 3.

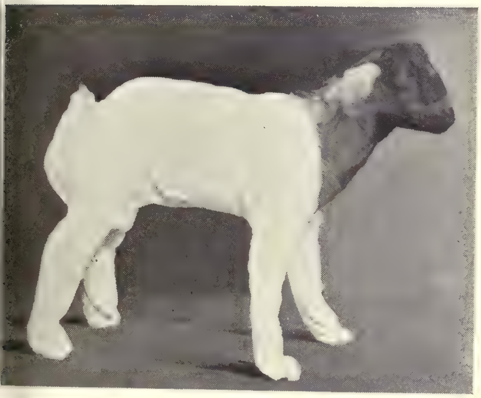


Fig. 4.

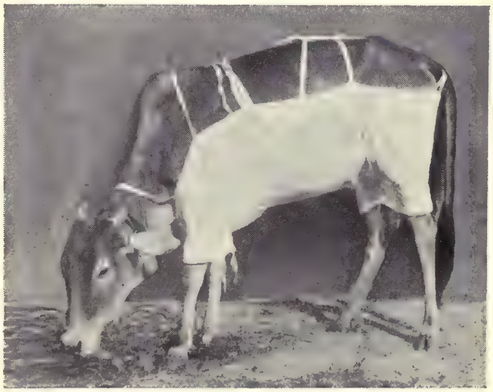


Fig. 5.

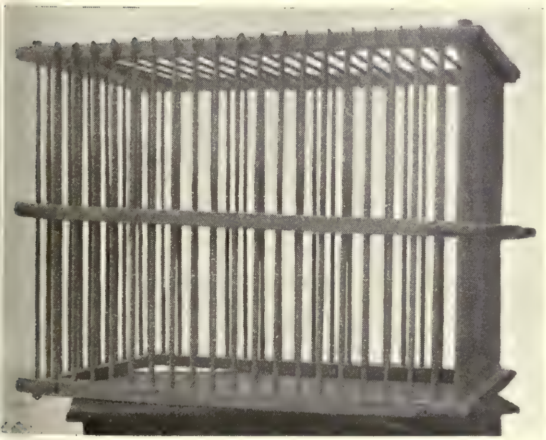


Fig. 6.

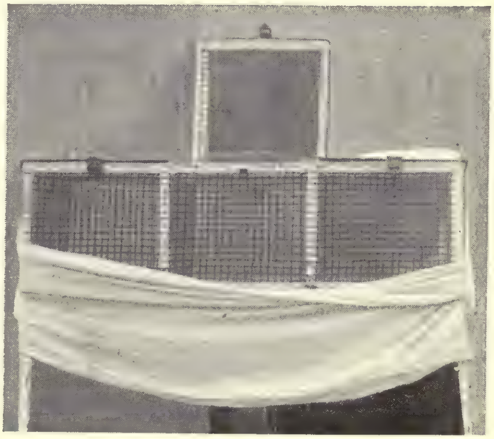


Fig. 7.

if they are dropped indiscriminately on the dog; even if they are brushed off they fall on to the straw and very soon come again in contact with the animal. This method of using straw is applicable in the manipulation of many other ticks.

After the ticks have been liberated in the cage the latter should be placed on a table. In the cage as elsewhere *R. sanguineus* always crawls upwards when it leaves the host. It is always best to take the dog out of the cage in order to feed it, and not to place the food in a tray in the cage; the straw is apt to become unnecessarily soiled, and some of the ticks may fall into the food. The cage should be cleaned once a day, and all faeces and soiled straw removed. Any ticks which have dropped off and crawled into crevices between the bars of the cage may be obtained by placing the cage on a white cloth on the floor and bumping it, when they fall on the cloth. The cloth bags should be changed every other day, as they become soiled with urine.

In the case of wild animals, which are difficult to handle, as for instance the jackal, young individuals should be obtained whenever possible; if this cannot be done the following method of handling the adults is successful and gives the minimum of trouble. The animal is placed in a cage specially devised for the purpose, and depicted on Plate LXXXII, fig. 6. The cage measures 2½ ft. × 1½ ft. × *22* in. and has iron bars ⅜ in. thick and 1¼ in. apart fixed into holes in the wooden framework; it has a foot-board made of wood with holes at the sides through which the iron bars pass, so that with the assistance of handles at each end it can be raised or lowered to any position. Iron bars similar to those at the sides are fixed horizontally into the top of the frame; these can be removed, as they are only kept in position by ⅜ in. nuts. The animal stands on the foot-board which, when raised, presses it against the iron bars on the top of the frame and renders it powerless; any of the bars can now be removed to give access to any part of the animal. The ticks are dropped on to straw placed on the foot-board, and the food is introduced from the top by taking out some of the bars; mongooses, civet cats and other fierce animals, which cannot be handled in the ordinary cage, may be kept in this one.

Those ticks of the genera *Rhipicephalus* and *Margaropus* which are parasitic on the larger farm animals demand a different form of technique.

Cattle ticks. R. appendiculatus

The larvae of *R. appendiculatus*, *R. simus* and *R. capensis*, all of which are common cattle ticks in South Africa, drop off their host when full-fed. According to Lounsbury the larvae and nymphs of *R. appendiculatus* attach themselves to almost any part of the body, but the adults seem to prefer the hairy margins of the ears ; frequently they may be seen attached to the scrotum and around the udder. Nuttall has recently studied the life history of *appendiculatus* ; his observations are here summarized. The larvae remain on the host from 3 to 7 days, the nymphs from 5 to 11 days and the female from 6 to 14 days. Unfertilized females may remain attached as long as 24 days. Oviposition begins from 6 to 23 days after the female drops off, and lasts from 15 to 56 days, during which time from 3,000 to 5,770 eggs are laid ; the eggs hatch out in from 32 to 65 days. The minimum time required for *appendiculatus* to complete its life processes is about 147 days.

The larvae of *simus* and *capensis* will not attach themselves to cattle, but according to Lounsbury they will feed on the dog ; the nymphs of *simus* prefer to attach themselves to the feet and tails of cattle ; those of *capensis* are usually found on the under parts, the dewlap, the udder, the scrotum and occasionally the tail.

In carrying out experiments with *appendiculatus* the larvae should be placed either on the ears of a cow or on the abdomen in the neighbourhood of the external genitals. In the case of the ear an *ear bag* is employed ; it should be sufficiently long to comfortably pass over the ear. A narrow hem is made at the base and a piece of elastic a little smaller than the circumference of the ear is let into it ; a tape should be attached on each side of the base of the bag and tied round the neck of the animal in order to keep it in position. It is important not to have the elastic too tight or the ear may become oedematous. These bags are equally suitable for enclosing the heads of fowls in connection with experiments with *Argas* ; in this case the tapes are crossed and tied under the wings. The same bag is also suitable for enclosing the tail of a goat, in which case the tapes should be much longer, as they are crossed over the sacrum and tied under the abdomen.

The larvae, nymphs or adults are dropped into the bag, which is then tied over the ear ; when all the ticks have become attached the bag may be removed until the ticks are about to drop off, when it is re-applied ; the replete ticks drop into the bag, from which they can be readily obtained.

The nymphs and adults of *simus* and *capensis* may be allowed to fix themselves on the under surface of the abdomen of a calf ; the larvae should be placed with a dog in a cage as described for *R. sanguineus*. In applying ticks to the abdomen of a cow the following plan is adopted. A strong cloth bag is made to fit closely against the skin and to enclose

R. simus and R. capensis: Use of abdominal bag

the upper parts of the legs; running tapes are fitted to keep the leg openings secure so that the ticks cannot drop out. Such a bag is shown in Plate LXXXII, fig. 5; it will be noted that it reaches nearly up to the spine, where it is secured with several tapes. In the front it fits closely to the root of the neck and is kept in position by a tape. At the other end sufficient opening is allowed for the passage of urine and dung, and the tape holding it in position is passed over the tail. A small quantity of clean straw is now placed in the bag in contact with the abdomen, and the ticks are dropped on to it; as soon as they have all become attached the bag is removed. About twenty-four hours before they become replete—this can be judged by their appearance—the bag is re-applied and the ticks are collected as they drop off.

Scrotal or udder bag

Calf box

This type of bag is not suitable for male animals. For which a smaller bag is made so as to enclose only the scrotum; the ticks are applied in the same way. In each case it is important to place a collar on the neck of the animal; the one shown in figure 2, Plate LXXXII, is the type used at the King Institute for vaccinated calves; it prevents them from interfering with the bag. Placing ticks on a cow without a bag and keeping it in a stall is not satisfactory, as in many instances the ticks are either crushed or are lost when they drop off. When using the bag method it is advisable to keep the animal in a box, and this precaution is specially necessary when exact transmission experiments are being carried out, as stray ticks may find their way on to the animal and vitiate the results. A box suitable for this purpose is shown in fig. 2; it is made from ordinary deal-wood cases. All cracks and crevices are carefully filled up with putty and the inside is painted white. The box should be just narrow enough to prevent the animal from turning round. One end has a narrow opening which can be closed by a sliding door; the calf is so placed in the box that its tail end is next the opening—it is shown as the reverse in the figure—so that the urine and faeces are passed, for most part, just outside the box. The legs of the box are placed in large tins of water. The authors keep these boxes in a special room which has a cement floor, and a six inch drain running round it, in which a strong solution of cyllin is kept. No stray ticks can possibly find their way on to the animals. When the experiment is concluded the box is washed with boiling water and after an interval of a week it is ready for a new set of experiments. Several species of tick, particularly *Rhipicephalus haemaphsaloides* and *Haemphysalis bispinosa* have been placed on calves in these boxes, either with or without bags, and in each case almost all the ticks have been recovered when they dropped off.

R. evertsi and R. bursa

The larvae and nymphs of *R. evertsi* always attach themselves deep in the ear, and as soon as the nymphs are nearing repletion ear bags should be applied. The adults prefer the hairless parts of the body, particularly about the anus, udder or scrotum. *Rhipicephalus bursa* may be found attached to almost any part of the bodies of sheep and goats ; on the former it is often found about the neck and ears. The various stages may be placed on these animals either by using ear bags or by dressing the animal in a cloth garment as shown in Plate LXXXII, fig. 4. This method of dressing the goat was devised by Lounsbury in connection with his experiments with heartwater and *Amblyomma hebraeum*. The garment should be tied securely about the neck as well as across the back ; it can be used for the sheep also.

Margaropus annulatus and its varieties

In the case of *Margaropus annulatus* and its varieties, all of which are found on cattle, it is best to utilize calves and to place them in boxes as described above. These ticks are easy to manipulate, as they remain on the host throughout all their stages. Under natural conditions *annulatus* is always found attached to the abdomen of the calf in the neighbourhood of the udder or scrotum, though very occasionally it may be found at some other part. The larvae should be placed either in ear bags or abdominal bags, which are re-applied when the females are about to drop off.

The female of *Hyalomma aegyptium* can be collected from cattle by using an abdominal bag. The larvae and nymphs may be fed on hedgehogs and guinea pigs by keeping them in the small cages described above.

Genus Amblyomma A. hebraeum, the Bont tick

Lounsbury has studied the life history of *Amblyomma hebraeum* ; he utilized goats and sheep, dressing them in a garment, as figured on Plate LXXXII, fig. 4. The larvae, nymphs and adults usually drop off after four or five days, and are found in the cloth. When only a few ticks are used, they may be placed on the leg in a closely fitting stocking about twelve inches long, with a double foot and with a puckering tape at the top ; the foot is double to prevent its being worn through. When the ticks begin to drop off, the cloth or stocking should be examined every hour. In order to prevent the animal from nibbling at the cloth, Lounsbury recommends placing it in a stanchion, similar to that used for holding milch cows. The iron collar shown in Plate LXXXII, fig. 2 would answer the purpose equally well. In the case of *A. hebraeum* the success of any experiment with the adults depends on having both sexes on the animal, for the female wanders about looking for the male and will not become replete with blood until after copulation.

Those species of *Amblyomma* which are parasitic on the larger animals may be experimented with in the same way as that described for the species of *Rhipicephalus* and *Margaropus*. It is just as easy to apply ticks to a horse as it is on a goat, provided that the feeding habits, particularly the sites of attachment, are known. Those species of *Amblyomma* which are parasitic on reptiles may be manipulated in the way described for the species of *Aponomma*, to be mentioned presently.

Genus Dermacentor

With the exception of *Dermacentor nitens*, *D. nigrolineatus* and *D. albipictus*, all the species of *Dermacentor* drop off their host for each of the two moults. The life histories and habits of the more important species have been studied by Hunter and Hooker, and Bishop and Wood. *Dermacentor andersoni* may be bred on cattle in all its stages; it leaves its host to undergo both moults. *Dermacentor nitens*, the 'Tropical horse tick' as it is called in America, attaches itself almost exclusively in the ears of horses; it may, however, occasionally be found attached to the neck under the mane. It can be manipulated with great ease if it is remembered that it only leaves the host when the female is replete with blood; ear bags are therefore only required to place the larvae on the host and again just before the females become full-fed. *Dermacentor albipictus*, though usually parasitic on the moose and elk, is often found on the horse and on cattle; the ticks attach themselves on the neck and along the back, on the abdomen, between the legs and sometimes near the base of the tail. On cattle the larvae moult on the 8th day, the nymphs about the 20th day, and the females begin dropping off about the 40th day after the larvae are placed on the animal; an abdominal or scrotal bag is used just before the females become full-fed. *Dermacentor nigrolineatus*, like *albipictus*, passes both moults on the host; it can be bred in the same way on cattle. The larva moults about the 10th day, the nymph from the 18th day onwards; the females begin dropping off about the 30th day after the larvae are placed on the host.

In experimenting with the species of *Haemaphysalis* the worker should remember that most of them are feeble ticks and are very slow in their movements. They are easily dislodged, and when this happens it is almost impossible to get them to fix themselves again. The life history of *H. leachi* has been studied in great detail by Lounsbury and more recently by Nuttall. Like all the others of the genus it requires three host of the same or different species in order to complete its life history. It is easily reared, according to Nuttall, on a number of different hosts, such as the jackal, dog, ferret, hedgehog, goat and rabbit. The larva and nymph remain attached to the host 3 to 7 days (Nuttall); the female remains on the host from 8 to 16 days. Oviposition begins from the 3rd to the 15th day after the female leaves the host, the period depending on the temperature; each female lays from 2,400 to 4,800 eggs. This tick may be manipulated in the same way as the other dog tick, *Rhipicephalus sanguineus* (see page 642); unlike most of the species of the genus it appears to be an active tick.

Genus Haemaphysalis. H. leachi, the South African dog tick

Haemaphysalis punctata

Haemaphysalis punctata has recently attracted considerable attention in England owing to the experiments of McFadyean and Stockman, who were able to transmit *Piroplasma bigeminum* to cattle by means of it. Its life history has been studied by these observers and by Nuttall. Its normal host appears to be the sheep, though it occurs naturally on the hedgehog and in the laboratory will feed on the rabbit. The larva remains on the host from 4 to 7 days, the nymph for about a week and the female from 6 to 22 days. It may be manipulated without difficulty by using either ear, scrotal or udder bags.

Haemaphysalis bispinosa

Haemaphysalis bispinosa, a common cattle tick in India, nearly always attaches itself about the head of its host. It is best manipulated by placing all the stages in ear bags, not in scrotal or udder bags; the same applies to this species when the goat is used as a host. It is important to watch the ticks when they are nearing repletion, for this species, more than any other, may be readily lost or crushed. It is also found on the mongoose, attached to the margins of the ears. When using this animal it should be placed in one of the small cages, always taking the precaution to see that the underpan is removed and that the bags are frequently changed; in the cages *bispinosa* never attempts to climb upwards, but is always found on the cloth at the bottom.

Other species parasitic on small animals

In Madras there are two other species of *Haemaphysalis* (at present unidentified), one parasitic on the South Indian hare, *Lepus nigricollis*, and the other on the gerbil, *Gerbillus indicus*. The species on the hare is commonly infected with *Crithidia haemaphysalidis*, Patton. Hares should be kept in the larger iron cages, taking care to handle them as little as possible, as they are very wild and dash themselves against the bars. A large cloth bag is placed round the cage and the larvae, nymphs and adults collected as they drop off; the underpan should always be removed. The species parasitic on the gerbil is best studied by keeping the rats in an ordinary wire trap, which is placed in a cloth bag; the ticks nearly always fix themselves on the back of the rat just above the tail, sometimes also about the face. Hooker mentions a species of *Haemaphysalis* which is parasitic on quails and other birds in the Southern States of America. It seems probable that this tick passes its first moult on the host. If this proves to be the case this is the first example of the occurrence of such a habit among the species of *Haemaphysalis.*

Genus Aponomma: A. gervaisi, the common snake tick

Ticks of the genus *Aponomma* are peculiar to reptiles, and most of the common snakes and larger lizards are infested with them. In Madras there are two species, *A. gervaisi* and *A. pattoni,* both of which may be collected in all their stages from the rat snake, *Zamenis mucosus*; *A. gervaisi* is also common on the lizard, *Varanus bengalensis.* These large lizards are very easily kept in one of the iron cages, and can be fed on pieces of raw meat; all the stages of the ticks are recovered by placing the cage in a bag. On the lizard the majority of the ticks attach themselves around the base of the tail, though the larvae and nymphs may be found attached to the eyelids. The larvae and nymphs may remain on the host for several weeks, and the females for months, before they drop off; the males have been found to remain on the host for more than a year, and several times a lizard has been caught with a number of dead males still attached to its skin.

Method of handling and keeping snakes

In order to study the life histories of the species parasitic on snakes it is necessary to know how to handle these animals. In India the snake catcher usually brings the snakes in an earthenware jar, the mouth of which is covered with a cloth, and it is impossible to obtain the ticks if the snakes are left in these vessels. The snake must be examined to see whether it harbours ticks or not, and must be transferred to a cage suitable for the purpose of collecting the ticks as they drop off. The simplest way to get hold of the snake is to turn it out of the jar on to an open piece of ground and to catch it as follows:—The worker and his assistant—and the snake catcher—should each be armed with a stick a yard and a half long, forked at one end and flat at the other. The head of the snake is compressed between the arms of the fork, and then grasped behind the jaws with one hand, while with the other a firm hold is taken of the tail. A snake held in this way is powerless, and can be examined for ticks. If this manœuvre is carried out rapidly the snake is caught before it has realized what is happening. Sometimes, however, it is not caught at once and then endeavours to escape; in this case it should be followed up and the flat end of the stick placed firmly on its head. The important point to remember in catching snakes in this way is to act with rapidity and never to hesitate; most snakes, even cobras and Russel's vipers, are stunned for the moment when they are tipped out of the jar, and it is at this moment that one should act. The two species of sand snakes (***Eryx johni*** and ***Gongliophus conicus***) both of which often harbour ticks, are the easiest to handle and can be kept alive for long periods in captivity.

If the snake is found to be harbouring ticks it should be placed in a wire cage; the one figured on Plate LXXXII, fig. 7 consists of three compartments, and the meshes of the wire are just small enough to prevent the snake from squeezing itself through; most snakes make vigorous attempts to escape. The cage is surrounded by a bag into which the ticks fall when they leave the snake. Cobras are fed by giving them egg beaten up with milk through a glass funnel passed into the mouth; vipers will eat rats and frogs if placed in the cage; the rat snake, ***Zamenis mucosus***, will readily eat frogs and toads. Sand snakes may be fed on small lizards.

If the worker has a dead snake or lizard brought to him and finds it has a number of ticks on it, he should on no account attempt to remove them with forceps, as they are sure to be damaged. It is best to place the snake in a white cloth bag for two or three hours, at the end of which time all the ticks will have left the host and will be found crawling about the bag.

Before concluding this section some general points connected with tick experiments may be mentioned:—

1. Unless for some special reason, large numbers of ticks should never be placed on one host; they only irritate the animal, causing it to scratch them off, and may even in the case of small mammals and birds cause death from loss of blood. A definite number should always be used and those which have become attached noted; ticks often wander from the place where they first fixed themselves and select another site. In some cases, however, it is necessary to place a large number on an animal in order to be certain that it will become infected with some particular protozoal parasite. For instance, only a small percentage of the

larvae descended from a female tick which fed on a dog or cow only slightly infected with *P. canis* or *P. bigeminum* will be infected; in order to ensure success a large number of such larvae must be used in order to infect the animal.

2. In the case of transmission experiments with protozoal parasites every precaution should be taken to exclude stray ticks from the experimental animal. An animal should never be considered to be free from ticks as the result of an external examination; it should be isolated for at least a week or ten days in order to allow the larvae and nymphs to drop off. These stages are often difficult to find, especially when they bury themselves among the hairs. Male ticks often remain attached for months; little or nothing is known as to what part they play in the transmission of protozoal parasites.

3. When conducting experiments with small animals, such as the dog, in order to discover at what stage the infection is taken up and by which stage it is transmitted, the larvae, nymphs and adults should be placed with the animal and every one recovered when they become replete; they should not be allowed to undergo metamorphosis in the cage and then re-attach themselves to the animal. If this precaution is not taken it will be impossible to be sure which stage carried the infection; there are numerous possibilities, some of which are noted in Chapter XII.

INTERNAL ANATOMY

(PLATES LXXXIII, LXXXIV, LXXXV AND LXXXVI).

There are several valuable papers on the internal anatomy of ticks; most of these, however, are of the nature of monographs, and do not deal with the subject in a practical or indeed a simple manner. The most satisfactory way of studying the parts is to learn first to recognize them as they are exposed in a dissection, and this method will be adopted in the following account. The method of dissection will be described first.

Dissection

Partially fed females should be selected for dissection rather than replete specimens, as in the case of the latter the diverticula, owing to the large quantity of blood which they contain, frequently rupture and may spoil the preparation. After some practice on partially fed specimens the manipulations can be carried out rapidly, and even replete females can be dealt with. The dissecting trough described in Chapter XI is very convenient for ticks, but if one is not available a large watch-glass in which some dark plasticine has been moulded will answer the purpose. The trough should be three-quarters filled with saline solution.

The anterior part of the body of the tick is grasped between the thumb and fore finger of the left hand, and a thin slice of the posterior edge of the integument is cut off with one sweep of a fine pair of scissors; the cut should commence about the level of leg IV on the left side—the dorsal surface being uppermost—and is carried rapidly as far round to the other side as possible. If the specimen is much distended a pair of flat entomological forceps may be used instead of the fingers; they should be placed about the level of the anus, in order to press as much of the contents of the abdomen as possible towards the anterior end, so that they will not protrude when the cut is made. Even with a partially fed tick the ends of one or more of the diverticula almost invariably rupture, but if undue pressure is avoided only a small quantity of the contents exude and the specimen is in no way spoiled. The tick is now dropped into the saline solution in the trough and is arranged so that its dorsal surface is uppermost. If a species of Ixodinae has been selected a No. 20 entomological pin is passed through one side of the basis capituli, and the specimen is fixed firmly to the wax by bending the pin over; if the tick is a species of *Argas* or *Ornithodorus*, the pin should be passed through the fold of skin at the anterior edge. The trough is placed on the stage of a binocular dissecting microscope and the lowest pair of objectives used. The dorsal integument at the site of the cut is grasped with a pair of fine forceps held in the left hand, and with a dissecting needle in the right hand the ventral integument is pressed against the wax of the trough; the two portions of skin are now gently separated and one or more pins are passed through the ventral skin to fix it to the wax. The dorsal integument can be reflected up to the point where the cut ended; a needle with a cutting edge is then passed between the two surfaces, great care being taken not to damage the intestine, and a series of lateral cuts is made; in this way the dorsal skin is completely separated up to the anterior end, and it can be reflected and pinned down. The internal organs are now exposed. In the case of the Ixodinae it is important to remember that the skin readily tears away from the scutum, and that when this is reached, in the dissection of a female, only very slight traction should be applied.

As the dorsal integument is reflected off it will be found to be bound down by muscles, tracheae, strands of connective tissue, etc. All these structures should be detached close to the under surface of the dorsal integument with the aid of the needle. Special care should be taken not to damage the heart and aorta ; the former may be seen lying on the mid-intestine. When the dorsal integument has been completely reflected several pins are passed through the sides of the ventral skin in order to prevent it from curling up. All the remaining manipulations can be carried out with a needle and a pair of forceps. A glass pipette with a rubber teat should be kept ready for use, as it is often necessary to flood some particular part which has become obscured by the dark fluid from a ruptured intestinal diverticulum. Care should be taken to see that the needles have clean points, for if they are rusty the organs tend to stick to them.

In dealing with male ticks care must be taken not to rupture the delicate sexual organs; the tick should be held by the mandibles and hypostome with a pair of broad flat forceps while the initial cut is made. Most nymphs can be dissected in the same way as the adults, but instead of attempting to cut right round the margin only a small nick is made with the scissors, and the incision continued with sharp needles after pinning the specimen in the trough. There is no really satisfactory way of dissecting the larvae. Most of the internal organs can be pushed out through a small incision at the posterior end, the manœuvre being carried out in a drop of saline on a slide. The relations of the parts in the larva can only be studied in serial sections.

When the dorsal integument has been removed and all the connective tissue, etc., cleared away, the intestinal diverticula are hooked up with a bent needle and then slowly unravelled. They float up in the saline and can be pinned to one or other side. The salivary glands will now be seen stretching back from the mouth parts to the neighbourhood of leg IV. They will be recognized by their lobulated appearance and white colour. The salivary duct may be followed up to its termination in the floor of the buccal cavity. The anterior end of the mid-gut should now be lifted up and the delicate oesophagus exposed; it will be seen passing downwards from the ventral surface of the anterior end of the mid-intestine towards a large rectangular white organ, the brain, through which it passes ; it emerges again at the anterior end of the brain to enter the pharynx or pumping organ. This latter structure will be found lying on the ventral side of the basis capituli between the two mandibles. On lifting up the posterior end of the mid-intestine and turning it to one side the hind-intestine will be exposed; in most cases it is a narrow tube of a whitish colour, but in some species it may contain digested blood. It passes down to the posterior surface of the rectum; the two long Malpighian tubes enter the rectum on either side of it. The rectum will be recognized as a large grey or black sac lying about the middle of the ventral surface and at the junction of the middle and posterior parts of the body; it often has accessory diverticula, as in *Argas*, to be described presently.

The testis and ovary lie slung across the body above the posterior diverticula and rectum; the ovary is readily recognized by the presence of the ova.

The Alimentary Canal. The mid-intestine and its diverticula. Plates LXXXIII and LXXXIV

The alimentary canal consists of a central tube with a number of secondary branches or diverticula, which are blind sacs capable of great distension. The central tube is short and lies in the middle of the body; it extends in an antero-posterior direction and is here referred to as the mid-intestine. When the mid-intestine and its diverticula are full of blood they form distinct prominences on the dorsal surface of the tick.

The anterior end of the mid-intestine may divide into two sets of diverticula, an antero-lateral and a lateral set; in addition to some species (*Ornithodorus*) there is an antero-median branch. In *Argas persicus* (Plate LXXXIII, fig. 1) the antero-lateral diverticulum (a. l. d.) passes forwards and outwards and divides into three branches. The anterior branch (a. b.) passes directly forwards and divides into three short branches; the external of these ends opposite coxa I, the middle, often the longest, bends inwards near its extremity and ends near the pharynx; the internal branch also ends in the same situation. These secondary branches are very constant in their arrangement.

The middle branch (m. b.) of the antero-lateral diverticulum passes outwards and soon divides into three short finger-like processes. The posterior branch (p. b.) is much longer and passes backwards and outwards towards leg IV; it then bends inwards and divides into two short branches.

In *Ornithodorus savignyi* and *O. moubata* the mid-intestine also gives off an antero-lateral branch (fig. 4, a. l. d.), which after a short outward course sub-divides into an anterior and a posterior branch. The anterior branch (a. b.) passes forwards and divides into three secondary branches as in *Argas persicus*. The posterior branch (p. b.) extends outwards and divides into two long branches, both of which pass downwards and inwards to end behind the salivary gland; it is not uncommon to

PLATE LXXXIII

Figure 1. Superficial dissection of *Argas persicus*, ♀, displaying the alimentary tract. × 12.

Figure 2. Deep dissection of same, displaying the reproductive organs. × 12.

Figure 3. Dissection to expose triangular area containing the brain of *Argas persicus* (see page 659). × 15.

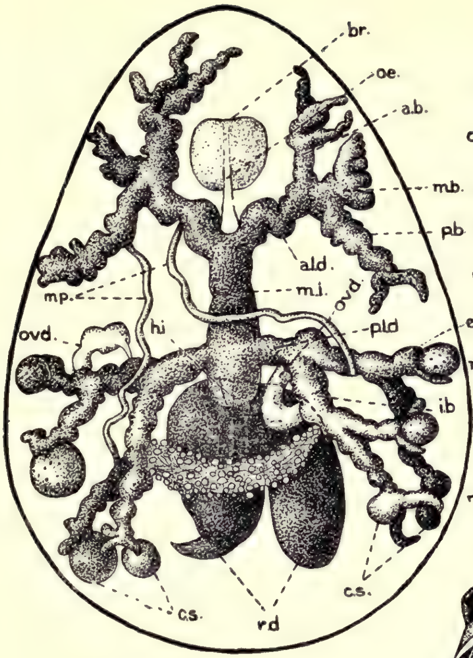
Figure 4. Superficial dissection of *Ornithodorus savignyi*, ♀, displaying the alimentary tract. × 9.

Figure 5. Deep dissection of same, displaying the reproductive organs. × 9.

Reference letters

a.b.	Anterior branch of antero-lateral diverticulum.
a.g.	Accessory gland.
a.m.d.	Antero-median diverticulum.
a.l.d.	Antero-lateral diverticulum.
br.	Brain.
chp.	Chitinous plate.
cg.	Coxal gland.
cs.	Cystic swellings.
eb.	External branch of postero-lateral diverticulum.
e.p.d.	External branch of posterior diverticulum.
ga.	Genital aperture.
go.	Gene's organ.
hi.	Hind intestine.
ib.	Internal branch of postero-lateral diverticulum.
i.p.d.	Internal branch of posterior diverticulum.
l.d.	Lateral diverticulum.
m.b.	Median branch of antero-latera diverticulum.
md.	Mandibles.
mi.	Mid-intestine.
mp.	Malpighian tubule.
o.	Ovum.
oe.	Oesophagus.
ovd.	Oviduct.
ov.	Ovary.
p.	Palp.
pb.	Posterior branch of antero-latera diverticulum.
ph.	Pharynx.
r.	Rectum.
rd.	Rectal diverticula.
sd.	Salivary duct.
sg.	Salivary gland.
tr.	Tracheae.
ut.	Uterus.
va.	Vagina.

PLATE LXXXIII.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oe.
a.b.
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pb
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ovd
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ovd.
hi
i.b
c.s.
c.s.
r.d

Fig 1.

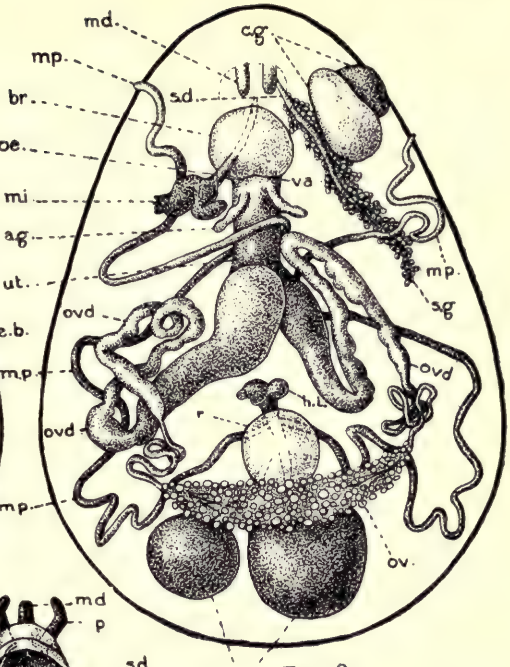
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Fig. 2

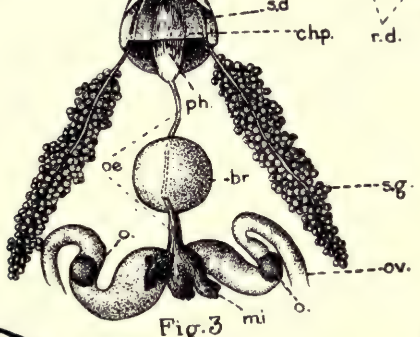
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Fig. 3

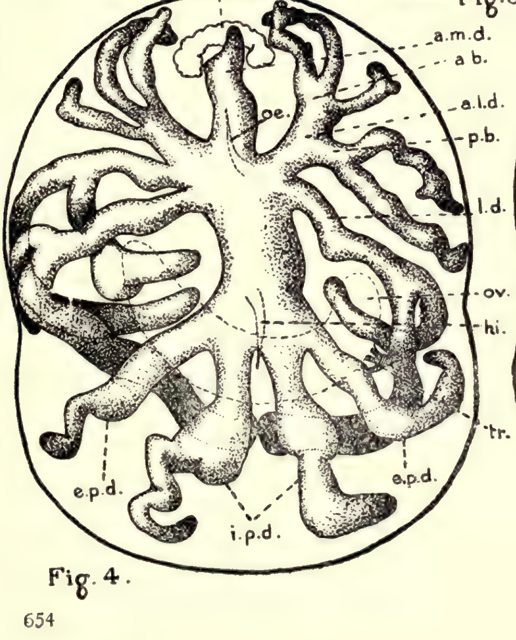
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Fig. 4.

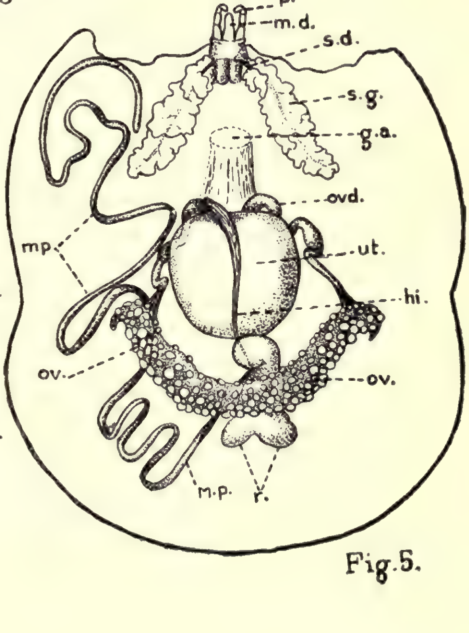
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Fig. 5.

find one of the posterior branches arising almost directly from the mid-intestine (Plate LXXXIII, fig. 4, left side).

In *O. savignyi* and *O. moubata*, in addition to the antero-lateral diverticulum, there is a true lateral sac. (fig. 4 l. d.) This is a long tube which passes outwards towards the point of origin of the tracheae from the spiracles, where it divides into two branches. One of these, usually the shorter, passes inwards towards the mid-intestine, then turns upwards behind it and ends near the brain. The larger branch passes directly backwards and ends near its fellow of the opposite side behind the posterior diverticula. In *O. savignyi* and *O. moubata* there is also a short antero-median diverticulum (Plate LXXXIII, fig. 4, a. m. d.) ; it extends straight forwards to lie over the mandibles and ends near Gene's organ (g. o.), to be described presently. This branch is not represented in any of the other ticks examined.

In *Margaropus annulatus* the antero-lateral diverticulum (Plate LXXXIV, fig. 1) extends for a short distance directly outwards and then divides into three branches. The first or anterior branch (a. b.) is short and passes forwards to end, with its fellow of the opposite side, near the pharynx. The second or median branch (m. b.) extends outwards and a little upwards, and turns inwards and backwards at the level of leg II to end under the salivary gland ; as a rule it is a long branch. The third or posterior branch (p. b.) passes downwards and backwards and soon gives off a lateral branch, which turns upwards and ends near the second branch of the antero-lateral diverticulum. About the level of leg III the posterior branch ends by dividing into two secondary branches ; the external of these passes downwards and backwards to the posterior border, where it turns upwards to end near the salivary duct. The internal branch turns in towards the mid-intestine, then bends upwards, and ends near the origin of the oesophagus from the mid-intestine. In *M. annulatus*, as in *O. savignyi*, the two sides are often not symmetrical ; for instance, the third main branch of the antero-lateral diverticulum on one side may extend for some distance before it gives off any branch, and on the opposite side it may divide up almost immediately after its origin from the main trunk.

In *Hyalomma aegyptium* (Plate LXXXIV, fig. 4) the antero-lateral diverticulum (a. l. d.) is arranged on much the same plan as that in *M. annulatus* ; in this case, however, the third branch extends for a considerable distance before it divides into its secondary branches.

According to Samson, who has studied the internal anatomy of *Ixodes ricinus*, the antero-lateral diverticulum in this species is much simpler ;

it divides into two branches, both of which pass backwards and outwards, the upper one to end near leg IV, the lower to turn inwards and backwards and to end at the posterior border.

Posterior diverticula

In *Argas persicus* the mid-intestine terminates in a round cul-de-saç which is in reality the first part of the hind-intestine. A short broad posterior or postero-lateral diverticulum (p. l. d.) arises from each side of the mid-intestine a little above its termination; after a short course outwards each tube passes backwards and divides into two main branches, each of which splits into two secondary branches. The main external branch goes outwards and then backwards to the posterior border, where it turns upwards to end on the ventral surface of the body; the main internal branch passes backwards, and at the posterior border turns upwards, its branches ending in the vicinity of the rectum. The main branches, together with their secondary branches, occupy the posterior third of the body when full of blood.

In *O. savignyi* the mid-intestine ends directly in four large posterior diverticula (Plate LXXXIII, fig. 4), which arise close together from the end of the intestine and are unbranched. They pass backwards to the posterior border and then turn upwards to end near the rectum.

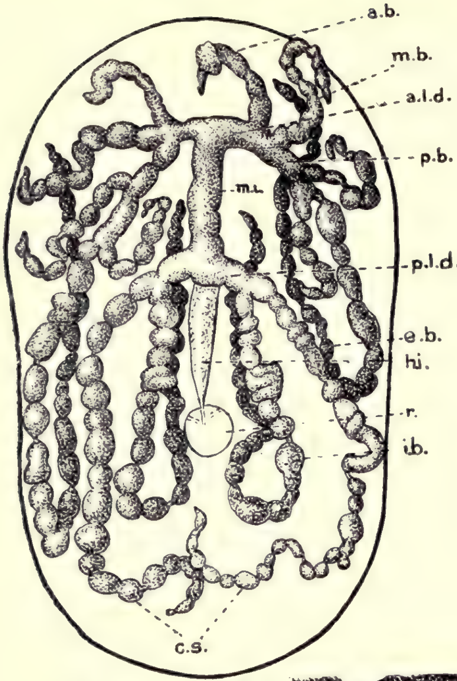
In *Margaropus* there are two main posterior diverticula (Plate LXXXIV, fig. 1), which arise from the sides of the mid-intestine; after a short course outwards they divide into two long branches, the external of which runs outwards and then backwards, and turns upwards at the posterior margin to end near the rectum; the internal branch also goes backwards parallel to the hind-intestine, and turns upwards on reaching the posterior margin to end at the side of the mid-intestine.

Much the same arrangement is seen in *Hyalomma aegyptium* (fig. 4); the posterior diverticula, however, instead of arising each from a common trunk, arise separately from the end of the mid-intestine as in *O. savignyi*. They are very long, and the internal pair pass backwards below the ovary on each side of the rectum to end near the anterior end of the mid-intestine.

In *Ixodes ricinus*, according to Samson, there are also four posterior diverticula which arise separately from the mid-intestine. They pass backwards parallel to each other and turn downwards and upwards on reaching the posterior margin; they end behind the ovary.

From the above description it will be seen that the general arrangement of the alimentary tract is very similar in the Argatini and Ixodini; in both there is an anterior and posterior set of diverticula with one or

PLATE. LXXXIV.


a.b.
m.b.
a.l.d.
p.b.
m.i.
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hi.
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c.s.

Fig 1

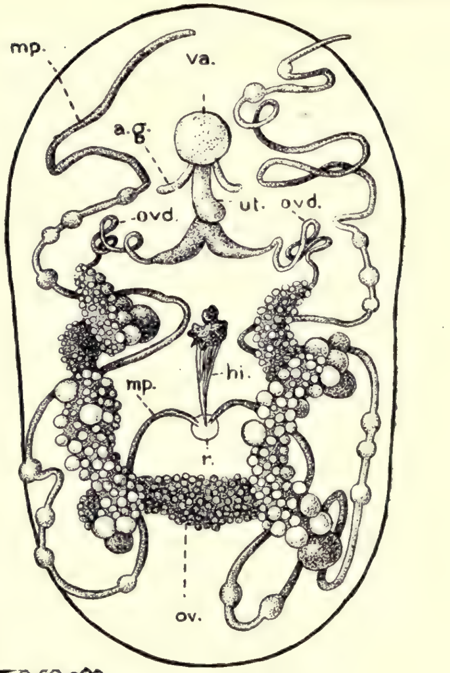
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Fig. 2.

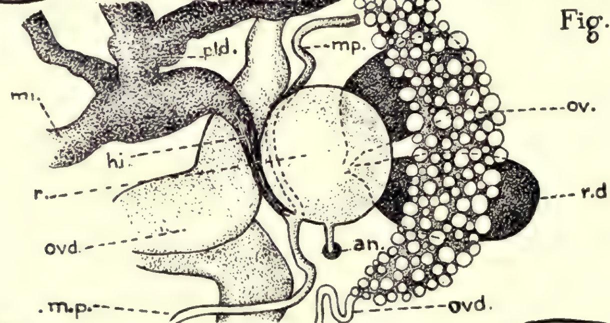
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Fig. 3.

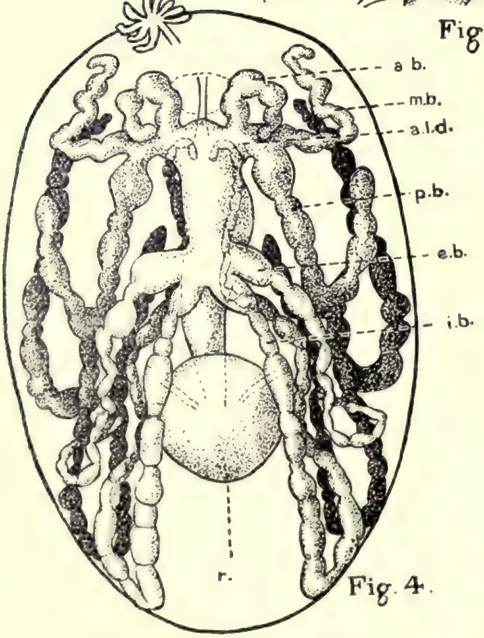
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Fig. 4.

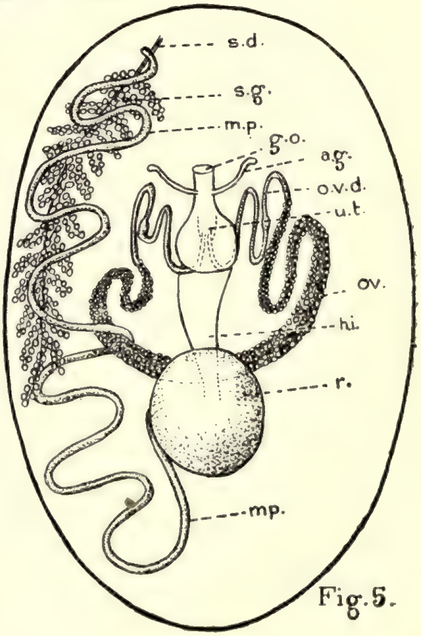

s.d.
s.g.
m.p.
g.o.
a.g.
o.v.d.
u.t.
ov.
hi.
r.
mp.

Fig. 5.

PLATE LXXXIV

Figure 1. Superficial dissection of *Margaropus annulatus*, ♀, displaying the alimentary tract. × 12.

Figure 2. Deep dissection of same, displaying the reproductive system. × 12.

Figure 3. Side view of dissection of *Argas persicus*, showing relations of hind intestine, rectum, ovary, etc. × 15.

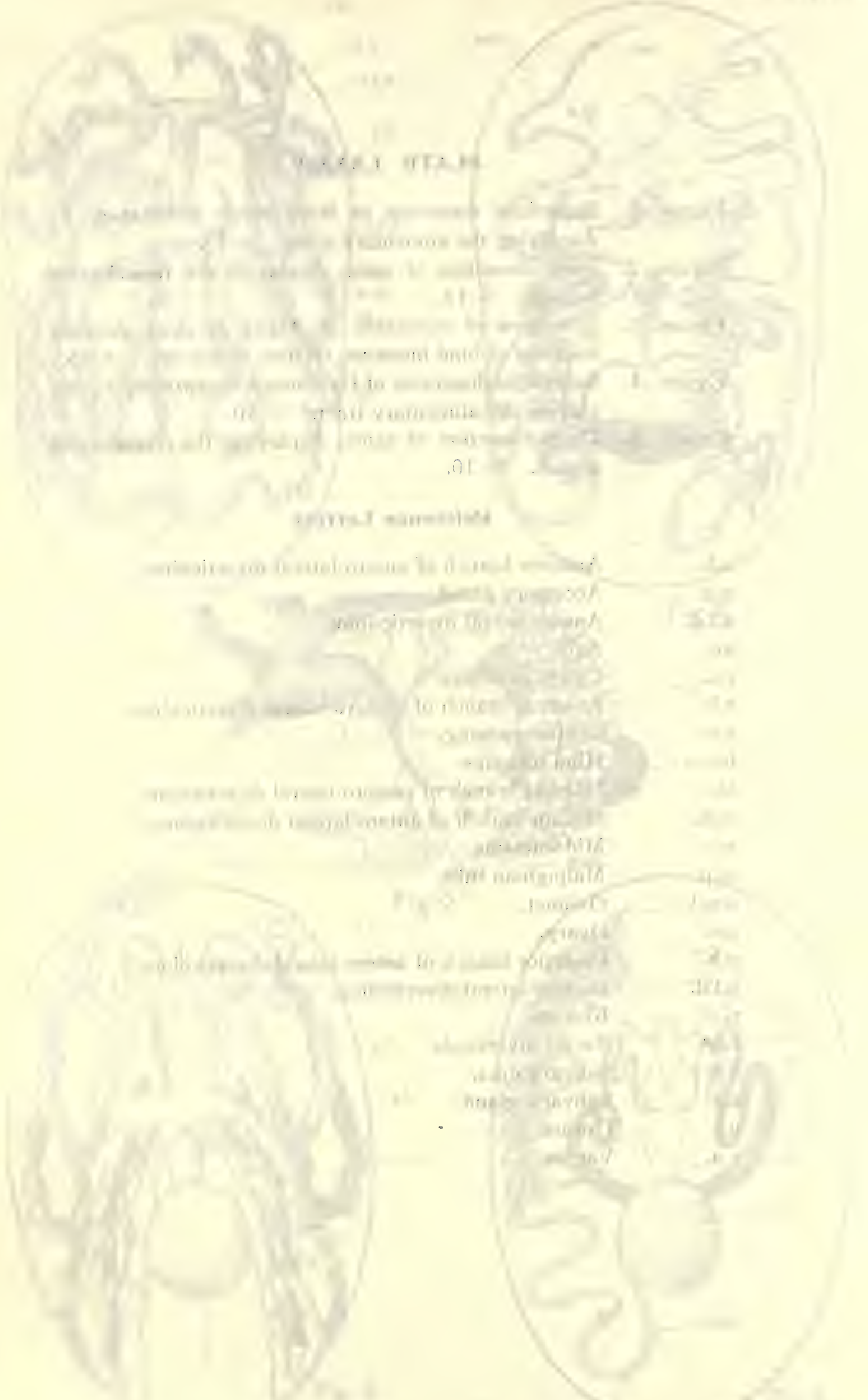
Figure 4. Superficial dissection of *Hyalomma aegyptium*, ♀, displaying the alimentary tract. × 10.

Figure 5. Deep dissection of same, displaying the reproductive organs. × 10.

Reference Letters

a.b.	Anterior branch of antero-lateral diverticulum.
a.g.	Accessory gland.
a.l.d.	Antero-lateral diverticulum.
an.	Anus.
c.s.	Cystic swellings.
e.b.	External branch of postero-lateral diverticulum.
g.o.	Genital opening.
h.i.	Hind intestine.
i.b.	Internal branch of postero-lateral diverticulum.
m.b.	Median branch of antero-lateral diverticulum.
m.i.	Mid-intestine.
m.p.	Malpighian tube.
o.v.d.	Oviduct.
o.v.	Ovary.
p.b.	Posterior branch of antero-lateral diverticulum
p.l.d.	Postero-lateral diverticulum.
r.	Rectum.
r.d.	Rectal diverticula.
s.d.	Salivary duct.
s.g.	Salivary gland.
u.t.	Uterus.
v.a.	Vagina.

PLATE LXXXIV.



more secondary branches; while in the Argatini, at least in *Ornithodorus*, there is in addition an antero-median and a true lateral branch. In the Argatini the secondary branches are short, stout, and often very irregular in outline; in the Ixodini they are narrower and very much longer, many of the secondary branches, which are difficult to unravel, reaching as far as the brain. In both the Argatini and Ixodini peristaltic movements are well marked in the mid-intestine, the blood being driven into the diverticula. In the Ixodini the diverticula often exhibit a curious appearance, being constricted in parts to form lobulations; these are also seen in the Argatini, but the lobulations are much larger, (in *O. savignyi* for instance) so that the diverticula have a ballooned appearance; at first sight the alimentary tract appears to consist of a collection of cystic bodies.

The hind-intestine. Plates LXXXIII and LXXXIV

The *hind-intestine* arises from the posterior surface of the mid-intestine a little above its termination, either from its middle or from one side. It is displayed either by cutting off the posterior diverticula, or by reflecting them and then lifting up the posterior end of the mid-intestine. The hind-intestine will be recognized as a narrow tube passing downwards and backwards to end on the posterior surface of the rectum. In *O. savignyi* and *O. moubata* it consists of a delicate white cord and is functionless; it passes over the uterus and dips down below the rectum to end on its posterior surface. In *Argas persicus* it is a much larger structure, is broad at its origin from the mid-intestine, and narrows somewhat as it passes down to end on the posterior surface of the rectum; it nearly always contains black digested blood and is in this tick a patent tube; this is demonstrated by the fact that an adult female, kept in a test tube, passes out black faeces.

In *Margaropus* and *Hyalomma* the hind-intestine (Plate LXXXIV, figs. 1, 2, 4 and 5) is broad at its upper end, which often contains black digested blood; it soon, however, narrows down to a delicate cord at its point of insertion into the rectum; as in *O. savignyi*, it is functionless.

The rectum

The rectum lies in the middle line, about the junction of the middle and posterior third of the body and just below the uterus. It may consist only of a single round sac or there may be in addition one or more secondary diverticula connected to the main sac by narrow tubes. In *Argas persicus* (Plate LXXXIII, figs. 1 and 2; Plate LXXXIV, fig. 3) there is a large central sac and two diverticula; both the main sac and its diverticula exhibit varying degrees of distension, but always contain black digested blood. In *Ornithodorus* the central sac is smaller and has a single posterior diverticulum (Plate LXXXIII, fig. 5), which is often split at its extremity into two short branches ; it always contains a white fluid—the excretion of the Malpighian tubes.

In *Margaropus* and *Hyalomma* the rectum consists of a single sac (Plate LXXXIV, figs. 1, 2, 4 and 5) lying in the same situation as that of *Argas* and *Ornithodorus* ; like that of the latter it contains a white fluid.

The Malpighian tubes

On reflecting the dorsal integument the Malpighian tubes are seen for a short part of their course lying over the mid-intestine ; they will be recognized by their yellowish white colour and by the fact that when punctured a thick chalky substance oozes out. Each tube begins blindly in the anterior part of the body in the neighbourhood of the antero-lateral diverticulum. From this point it passes outwards below the salivary gland, around the free end of which it may coil more than once. It then comes into contact with the main tracheal trunks as they leave the spiracle, from which it receives a liberal supply of tracheal twigs, and, turning inwards, makes several coils round the branches of the antero-lateral diverticulum. It next passes upwards and coils round the oviduct and the upper part of the ovary, and on reaching the dorsal surface comes into close relationship with the mid-intestine and the dorsal blood vessel ; here it may make one or several turns round the mid-intestine. It then passes backwards and dips down towards the ventral surface, forming a number of convolutions in the posterior part of the body, where it comes into direct contact with almost all the posterior diverticula and the ovary. Finally it enters the rectum on its ventral surface by an opening close to that of its fellow of the opposite side.

Owing to the great length of the Malpighian tubes and to their complicated course they come into close relationship with almost every organ, and more particularly with the intestinal canal and its diverticula, around which they coil in several places. From this it can be readily understood that a motile parasite, such as a spirochaete, may easily pass into the tubes either from the haematocoele or from the intestinal canal. It should be noted also that the tubes exhibit great functional activity ; during the period of oviposition they are loaded with secretion, and can be seen through the dorsal integument as broad yellowish white bands.

In order to study the anterior part of the alimentary tract, the antero-lateral and antero-median diverticula should be cut off close to the mid-intestine with a pair of scissors; all tracheal twigs, the Malpighian tubes, connective tissue and other structures should be removed. If necessary the parts should be flushed with saline and fresh solution added to the trough. On lifting up the anterior end of the mid-intestine the delicate oesophagus is seen entering it on its posterior surface. When this is followed forwards it is found to pass downwards and to enter a large white structure, the brain, from the anterior end of which it emerges to unite with the pharynx. The brain should be carefully lifted up and the nerves passing from it divided; the adjacent parts should be cleared of all tracheae, care being taken not to damage the salivary ducts. When this preliminary dissection has been completed it will be seen that a triangular area has been exposed (Plate LXXXIII, fig 3). The apex of this triangle is situated at the base of the capitulum and of the chitinous mouth parts; laterally it is enclosed by the salivary glands and their ducts, and posteriorly by the oviducts and mid-intestine. The brain lies deep down about the centre of the area, and is traversed from before backwards by the oesophagus as it passes to enter the mid-intestine; the pharynx lies at the apex of the triangle and may be recognized by its fusiform shape. Although the formation of the buccal cavity and the adjacent parts is most satisfactorily studied in transverse and longitudinal sections of the capitulum, the general arrangement and relations of the various structures can be made out in an ordinary dissection.

The fore-intestine: dissection to expose the parts

For descriptive purposes the buccal cavity may be divided into two parts, only one of which, the posterior, is completely closed. The anterior part is a flat tube, the dorsal wall of which is formed by the apposition of the two mandibles and their sheaths, the ventral by the hypostome. In the normal resting condition this tube is open at the sides (Plate LXXXV, fig. 2), and the two walls can be separated by a needle. When the tick is attached to its host, however, the mouth parts are embedded in the skin, which closes the sides of the buccal cavity. The posterior part is closed at all times. The mandibular sheaths fuse with each other in the middle line, and with the hypostome at the sides, about the level of the lower third of the second palpal segment, though the exact position varies in the different species; the dorsal integument of the basis capituli passes forwards to fuse with the basal joints of the palps and the sheath of the mandibles, and the ventral integument blends with the hypostome. The chitinous ring which is thus formed is spoken of

The buccal cavity. Plate LXXXV

as the *mouth ring*, and at this point the buccal cavity becomes widened out.

At the level of the first palpal segment the buccal cavity becomes enclosed completely (fig. 3) by the dorsal and ventral integument of the basis capituli, and about this level the basal end of the hypostome divides into two processes, the posterior of which blends with the ventral body wall, while the anterior is continued backwards as the ventral wall of the buccal cavity (Plate LXXXV, fig. 1). In a median longitudinal section a little to one side of the middle line (fig. 1) the buccal cavity is seen as a long tube bayed out at its posterior end; it is bounded dorsally by the mandibular sheaths and the mandibles, ventrally by the hypostome, and laterally by the strong fold of integument formed by the junction of the sides of the hypostome with the skin of the last palpal segment (fig. 3). The posterior end is closed by a strong bar of chitin formed by the internal extension of the basal joint of the palpal segment and by the base of the hypostome; from the posterior surface of this bar a horizontal plate of chitin projects backwards into the anterior end of the body cavity (Plate LXXXIII, fig. 3), dividing it into two compartments. The bulbous ends of the mandibles lie on the plate in the dorsal compartment and the pharynx lies in the ventral. The salivary ducts enter the mouth ring at the sides of the plate which supports them, and open into the sides of the bayed-out end of the buccal cavity.

Samson, in her account of the buccal cavity of *Ixodes ricinus*, figures and describes an elastic flap of chitin which extends forwards from the ventral wall of the buccal cavity and divides it into two portions. She regards the dorsal chamber into which the salivary ducts open as the salivary receptacle; the ventral chamber contains the opening of the pharynx or pumping organ. She believes that the chitinous flap acts as a valve, and that the saliva, as it flows from the ducts situated above and behind it, presses it down and closes the opening into the pharynx; in this way the saliva is prevented from passing directly into the pharynx.

Mechanism of the mouth parts

The mouth parts of ticks are adapted for the purpose of piercing the skin and at the same time fixing the parasites to their hosts. The mechanism may be studied by placing an unfed tick, such as a female *Rhipicephalus sanguineus*, on the ear of a dog. After moving about for a short time, feeling the skin with the ends of the palps, the fourth segments of which are armed with well developed sensory hairs, a suitable spot is selected and the mouth parts lowered. The palps are then everted, and a firm hold

PLATE LXXXV

Figure 1. Longitudinal section through the capitulum of *Margaropus annulatus*, ♀, showing the buccal cavity with its bayed-out posterior end, into which the salivary ducts open. × 122.

Figure 2. Transverse section through the rostrum of *Aponomma gervaisi*, ♀, about the level of the middle of the second palpal segment—the palps are not shown—displaying the buccal cavity which is here open at the sides. × 240.

Figure 3. Transverse section through the rostrun of same, about the level of the first palpal segment; the buccal cavity is here closed in at the sides as explained on page 660. The section passes through the buccal cavity just anterior to the openings of the salivary glands. × 233.

Figure 4. Transverse section through the basis capituli of same just in front of the porose areas. Note the openings of the salivary ducts and the two portions of the buccal cavity. × 150.

Figure 5. Transverse section through the posterior portion of basis capituli of same showing the pharynx. × 150.

Figure 6. Hypostome of *Amblyomma testudinarum*, ♀, highly magnified.

Figure 7. Hypostome of *Ornithodorus savignyi*, ♀, highly magnified. Compare the poorly developed teeth with those on the hypostome of *Amblyomma testudinarum*.

Figure 8. Mandible of *Amblyomma testudinarum*, ♀, showing the digits, highly magnified.

Figure 9. Mandible of *Ornithodorus savignyi*, ♀.

Reference Letters

b.c.	Buccal cavity.	mi.	Mid-intestine.
br.	Brain.	oe.	Oesophagus.
cap.	Capitulum.	o.s.d.	Opening of salivary duct.
cl.sp.	Cellular space.		
d.	Diverticulum.	ph.	Pharynx.
d.b.c.	Dorsal buccal cavity.	r.md.	Retractors of mandible.
d.ph.	Dilators of pharynx.	sd.	Salivary duct.
g.a.	Genital aperture.	sh.	Sheath of mandible.
hy.	Hypostome.	v.b.c.	Ventral buccal cavity.
md.	Mandible.		

PLATE.LXXXV.

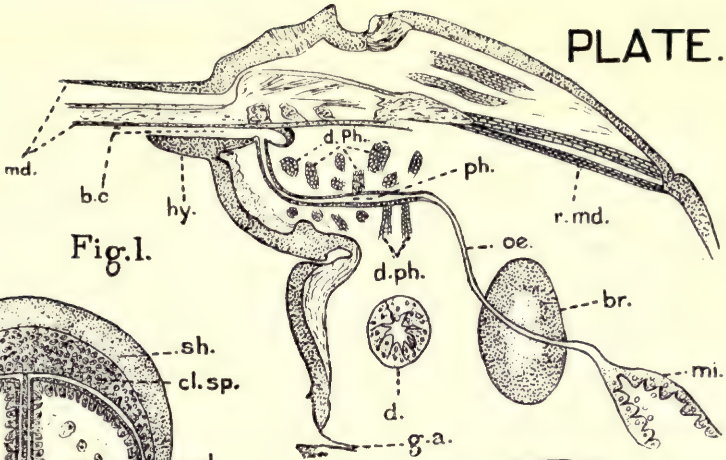

md.
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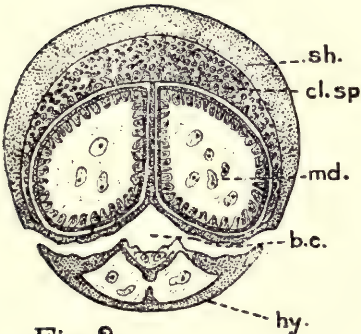
Fig.1.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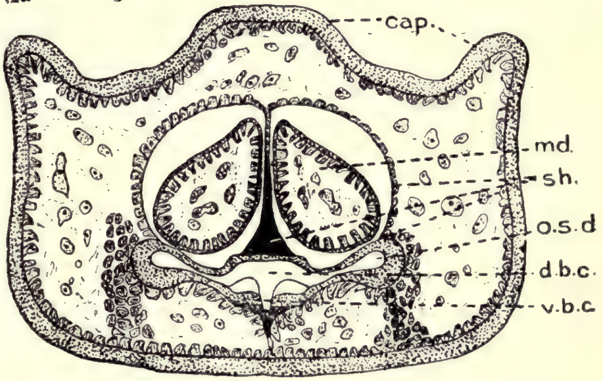
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Fig.4.

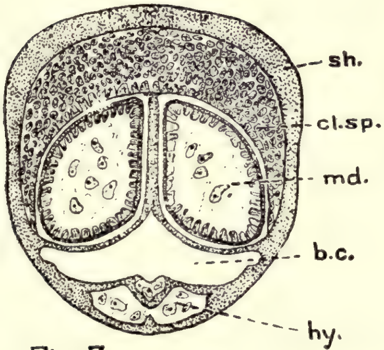
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Fig.3.

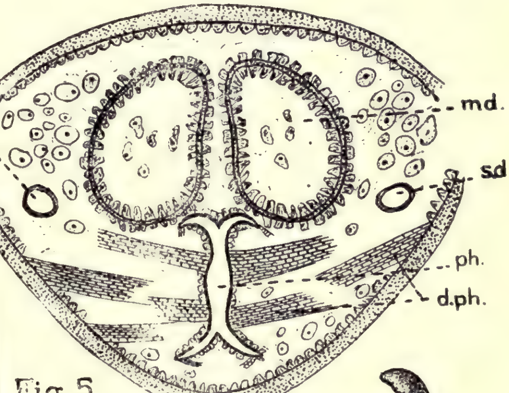
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Fig.5

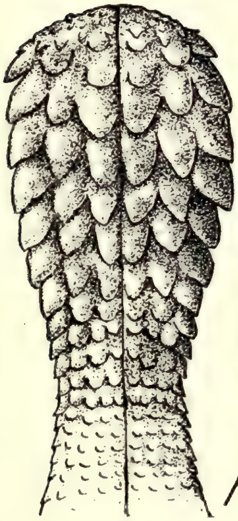

Fig.6.

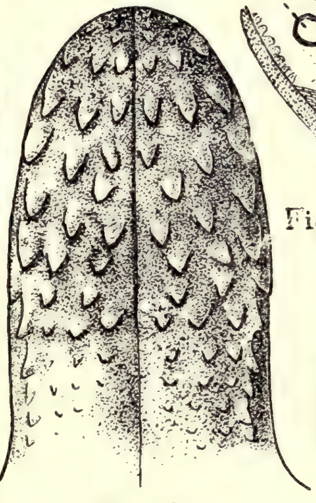

Fig.7.

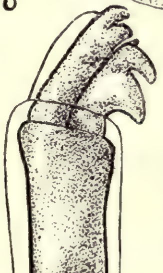

Fig.8.

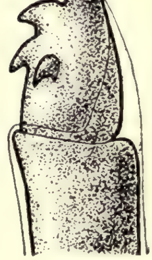

Fig.9.

of the skin having been obtained with the legs, the tick makes a steady forward thrust with its body, as a result of which the hypostome is driven into the skin. At the same time the mandibles are protracted and their digits extended, and the teeth brought into play. As the forward thrust is continued the hypostome is driven deeper into the skin until it is almost completely embedded. If an attempt is made to remove the tick it will be found to be firmly attached, the attachment being mainly due to the strong recurved teeth of the hypostome. This function of the hypostome is well exemplified in the various species. For instance, in the Argatini (Plate LXXXV, fig. 7), which feed rapidly and then leave their host, the teeth are poorly developed in comparison with those of the Ixodini (fig. 6) which remain fixed to the host for long periods; in the latter the teeth are formidable weapons and considerable force is required to detach them. In some genera, for example, *Haemaphysalis*, though the teeth are well developed, the hypostome is short and the tick is never able to obtain such a firm hold as in the species of *Amblyomma*, *Hyalomma*, and more particularly *Ixodes*, in which the hypostome is long and is armed with many rows of strong projecting teeth; for this reason *Haemaphysalis* is readily detached and therefore usually selects those parts of the skin where the host cannot very well scratch it off.

The hypostome is to be regarded as the fixing organ, and is not withdrawn or moved once the tick is fixed; the mandibles on the other hand are the true cutting organs, and they are only brought into further action when suction begins. The mandibles appear to be very similar in action to those of the Orthorraphic Diptera; protraction and retraction of the shaft, together with extension of the teeth on the digits, results in a saw-like movement which tears a hole in the skin. When the pumping action of the pharynx, to be described presently, comes into play the blood is drawn into the intestinal tract. The flow appears to be intermittent in the case of the Ixodini, a small quantity only being taken in at first; when the tick is fertilized it fills up in a short time, and then withdraws its mouth parts and crawls away.

The irritation produced by the penetration of the mouth parts into the skin, or the action of the salivary fluids, appears to produce in some species an inflammatory reaction which results in the whole of the capitulum being buried in scar tissue; this is commonly seen in the case of the male *Hyalomma aegyptium*.

The *pharynx* consists of chitinous plates welded together to form a long fusiform tube, which acts as the pumping organ. At the anterior end, which is U-shaped in cross-section, it opens into the buccal cavity at a right angle to the ventral wall of the latter (Plate LXXXV, fig. 1);

The pharynx

the opening consists of a V-shaped slit, the lateral arms of which are directed backwards. After the initial bend the tube passes first upwards and then straight backwards to become continuous with the oesophagus. In the main part of the tube the lumen is X-shaped on section (Plate LXXXV, fig. 5), with two dorsal and two ventral horns. The musculature is complex, and consists of sets of dilator muscles, passing between the dorsal and ventral walls of the capitulum and the plates which make up the sides of the pharynx, and in addition certain accessory bundles, which appear to act as sphincters. These latter pass between the dorsal and ventral horns on each side, and between the dorsal and ventral horns of the two sides in a transverse direction. In *Ixodes ricinus*, according to Samson, the structure of the pharynx is further complicated by the bifurcation of the dorsal horns, the secondary horns being also connected by small muscle bundles. The mechanism of the pharynx appears to be of the usual type, the dilator muscles, by withdrawing the plates from one another, producing the requisite negative pressure, while the sphincter muscles, acting in a peristaltic manner, assist in the propulsion of the fluid into the succeeding part of the gut.

The oesophagus. Plate LXXXIII, fig. 3

At the level of the posterior end of the mandibles, which, as noted above, project into the body cavity, the pharynx merges into the *oesophagus*; this at once dips downwards almost at a right angle and passes through the brain, emerging at its posterior border. After a short upward course it enters the mid-intestine on its ventral surface.

Histology of the intestinal canal and its appendages

The oesophagus is lined by single layer of high columnar epithelial cells, which are covered internally by a chitinous intima. External to the delicate basement membrane there is a layer of circular muscle fibres. At the point where the oesophagus enters the mid-intestine the cells are heaped up to form a rudimentary proventriculus, and the circular muscle fibres are more abundant; the cells of the oesophagus end abruptly at its junction with the mid-intestine. The mid-intestine and all the diverticula are lined by a single layer of somewhat irregularly shaped cells (Plate LXXXVI, fig. 1), the shape of which depends to a large extent on the stage of digestion. They may be either flattened out to form a continuous layer as in full-fed specimens, or they may exhibit all sizes and shapes and project from the wall, as in specimens in which digestion is well advanced. In both cases the cells have a centrally placed nucleus and contain spherical globules, yellow in the fresh condition and intensely black when stained with haematoxylin.

The wall of the rectum is very thin, and is lined by a single layer of flattened cells; these never show much variation in shape. The Malpighian tubes are lined by a single layer of large columnar or cubical cells, which become flattened out in the distended state of the organs. Their nuclei are very large and of a vesicular nature, and the protoplasm has a striated appearance. The lumen of the tubes is occupied by masses of oval or dumb-bell-shaped crystals, believed to be of the nature of uric acid.

The process of digestion

The process of digestion has been studied by Samson in *Ixodes ricinus* and by Christophers in *Ornithodorus savignyi*. As the subject is of considerable importance, ticks being the invertebrate hosts of the Piroplasmata, which have an intracellular phase, their observations are here summarized.

On sectioning a piece of the mid-intestine or one of the diverticula—for the structure is the same in both—of a female just after metamorphosis and before impregnation, the black globules referred to above, which were produced during the digestion of blood in the nymphal stage, are seen to be present only in small numbers. The gut is sunk inwards and the basement membrane has a folded and pleated appearance. The cells are mostly small and contain many vacuoles; the nucleus is clear and has very little chromatin in it, so that the nucleolus is visible. In specimens which have been allowed to attach themselves to a host and to commence to suck blood, and removed after a short time, the lining cells are seen to be flattened out by the blood and to form a thin layer; if the tick is allowed to become almost replete with blood and then removed and a piece of the intestine sectioned, it will be seen that digestion has already commenced. The lining cells become elongated, project into the blood and become full of vacuoles and plasma fibrils. The blood soon becomes altered into a dark, red, sticky fluid, all its cellular structures becoming broken down and unrecognizable; at this stage digestion is completed and absorption begins.

As soon as the blood is broken up, and this takes place with great rapidity, the intestinal cells increase enormously in number and in size, and project into the lumen of the gut; between the large cells there are many smaller ones which take the place of the former as they become extruded. The large cells become filled with plasma fibrils, and their nuclei are pushed forwards so that they come to lie towards the periphery of the cells. The cells now begin to absorb the dark globules from the digested blood until they become completely filled. The globules become transformed into clear drops. In a suitable preparation the absorption of the globules from the blood and their transformation into clear droplets may be seen going on at the same time. The cells now project more and more into the lumen until they remain attached to the basement membrane only by a slender stalk; many of them become free in the lumen of the gut and their places are taken by fresh cells which have grown out of the small cells near the basement membrane. As absorption proceeds the clear globules become transformed into the yellow balls which are seen in the fresh condition in a tick recently changed from the nymphal stage to the adult. When all the blood has been absorbed the delicate intima lining the cells becomes detached and lies free in the gut; Samson compares it to the peritrophic membrane of the mid-gut of insects. It is interesting to note that Nuttall and Strickland have found that the intestine of *Argas persicus* contains an anticoagulin but no haemolysin.

Salivary glands and ducts: Plates LXXXIII and LXXXIV

The *salivary glands* lie in an oblique position on each side over the bases of the first three legs, and can be recognized by their characteristic appearance, very like that of a bunch of grapes in minature. At its anterior end each gland comes into contact with the base of the mandible of its side and externally with the coxal gland; the posterior or free end lies over the main tracheal trunks. Each gland consists of a number of lobules, made up of globular acini arranged about the central excretory duct; in addition there are a number of single-celled glands on the main duct and some of its larger branches. Each acinus is made up of two kinds of cells; one kind is situated at the opening of the acinus and the other at the base, and therefore spoken of as the 'fundus cells'. Both in starving and in fed ticks the cells at the mouth of the acinus contain large granules which stain deeply with haematoxylin. The fundus cells, on the other hand, have only a few granules in starving ticks, while in fed specimens they are often completely filled with clear globules of excretion, which stain only feebly with haematoxylin. The duct of the acinus begins as a narrow channel, soon developing into a definite duct lined by flat cells; it joins similar ducts to form a lobular duct which in turn receives other lobular ducts and then enters the main channel; in this way an arborescent appearance is produced.

The large single-celled glands consist of pyramidal cells with broad bases; their protoplasm consists of a peripheral zone and a middle zone.

According to Samson the former stains a brilliant yellow with picric acid and contains delicate threads and many granules. In a tick that is feeding, the middle zone is divided off from the marginal zone and is full of secretory globules; at the boundary between the two zones there are two or three sausage-shaped nuclei which contain large irregular masses of chromatin. Minute channels conduct the secretion from the middle zone to the marginal, where they join to form a single duct which opens into the main salivary duct on which these glands are situated.

In the larva the salivary glands are in an immature condition and are unbranched; as a rule only three or four acini are present. Their number increases in the nymphal stage and the glands become branched. In the adult stage the secreting elements are only fully developed just before and during the act of feeding. In the replete female (Ixodini) the glands soon break up into granular masses and finally disappear when the tick has begun laying her eggs.

Christophers, and Nuttall and Strickland, have shown that the salivary glands of ticks contain a considerable quantity of anticoagulin; the latter observers found that the anticoagulin present in the salivary glands of *Argas persicus* may delay coagulation of human blood for forty-five to ninety-five minutes or indefinitely.

The salivary ducts pass along the sides of the horizontal plate of chitin, and, piercing the mouth ring, open at the sides of the buccal cavity as described above (Plate LXXXIII, fig. 3).

The coxal gland

The *coxal gland* (Plate LXXXIII, fig. 2) is situated in the anterior third of the body just over coxae II and III and in close proximity to the salivary gland; it may be recognized by its white colour and by its rich tracheal supply. Each gland is of an irregular shape, and consists of one or more lateral lobules. On section the gland and its accessory lobules are seen to consist of a number of gland cells with large irregularly shaped nuclei. The protoplasm of the cells is filled with dense masses of supporting fibrils; minute excretory channels discharge the excretion from the cells into larger ducts, which open on the coxal joints. The exact function of this gland is unknown, but several observers have noted that a secretion exudes from it, in the case of *Ornithodorus savignyi* and *O. moubata*, during the act of feeding; Christophers states that the fluid is alkaline in reaction and contains an anticoagulin. The gland is present in all female ticks.

Gene's organ (Plate LXXXIII, fig. 4), also described as the *cephalic gland* (Christophers) and the *sub-scutal gland* (Samson), is a large glandular structure associated with the deposition of eggs, and is therefore only seen in the female; in the Argatini it is situated in the anterior end of the body above the capitulum and beneath the anterior diverticulum (*Ornithodorus*), and consists of a single sac-like gland; in the Ixodini it lies below the anterior end of the scutum and usually consists of four separate tubes. The gland follicles, which are lined by a single layer of columnar cells, only attain their full development just before the female begins to oviposit. In the Argatini the gland opens externally by a large transverse slit in the fold of skin dorsal to the capitulum; in the Ixodini the glands open by separate ducts in the fold between the capitulum and the scutum; their openings can be demonstrated by folding the capitulum back on to the ventral surface. The function of the sticky secretion which is discharged from Gene's organ is dealt with in connection with the process of oviposition.

Gene's Organ

The Respiratory System. The stigmal plate. Plate LXXV, figs. 4 and 5

The respiratory system, unlike that of the Insecta, consists of a single orifice on each side, situated on the *stigmal plate*, with a number of tracheae for the supply of the organs. In the Argatini the stigmal plate is usually small, and is situated a little anterior to coxa IV; in the Ixodini it is large and is situated behind and below coxa IV. The structure of the stigmal plate of *Haemaphysalis punctata* has been described by Nuttall in collaboration with Cooper and Robinson; that of *Ixodes ricinus* by Samson; their observations are here summarized.

The spiracle consists of an elevated chitinous plate of varying shape and dimensions and with a well-defined margin; in the adult stage it is longer than broad, while in the nymph the reverse is the case; the larva has no spiracles. The shape of the chitinous plate is of use in separating the genera, and its structure in recognizing the species, at least of the genus *Dermacentor*. Situated a little to one side of its centre and nearer the antero-mesial margin there is a dark raised area, named by Nuttall, Robinson and Cooper the *macula*; it is elliptical in outline and is pierced in the female by a slit-like opening termed by the above observers the *ostium* (stigmal pore of other authors), which is guarded externally by a raised lip acting like a valve; the ostium is absent in the male and the nymph. The marginal portion of the spiracle is of a dark colour, while the area between it and the macula is of a greyish colour and has many evenly distributed pores opening on its surface. On examining the surface of the spiracle with a lens dark and light spots may be made out; the latter represent the small pores of the superficial layer to be described presently, and the former the rods or pedicels which lie on the basal layer and which shine through. If the entire spiracle is examined after it has been cleared in caustic potash and mounted on a slide, it will be seen to be a complex structure made up of three superimposed layers, the relations of which are best studied in transverse and longitudinal sections. The superficial layer has a reticulated appearance, with circular meshes which represent the small pores the openings of which are seen on the surface as clear spots. Below the superficial layer there is the pedicel layer, which is traversed by delicate rods, the pedicels, which arise from the basal layer of the plate. The basal plate is composed of thick chitin and is pierced by minute pores which correspond in position to the superficial pores, but which are impervious to air. The pedicels themselves are triangular in section, and are fused together at their upper ends on the ventral surface of the superficial layer.

That part of the stigmal plate which lies below the macula has a different structure. It is formed of a columnar mass of connective tissue and muscle fibres which extend upwards from the soft structure beneath the spiracle. Nuttall and his collaborators have named this the *columella*. Surrounding the columella there is a circular air space, the *pericolumellar space*, which communicates with the spaces between the pedicels in the pedicel layer. The ostium or stigmal pore opens into the pericolumellar space on the inner side of the columella, and that portion of the pericolumellar space immediately below the ostium is continued downwards as a large chamber, and has been named the *atrium* by the above observers. The main tracheal trunks open separately into the cavity of the atrium, which is elliptical in cross section. Extending up the columella there is a muscular band which is inserted along the dorsal wall of the atrium, some of the fibres being inserted also into the superficial layer just below it. Nuttall and his collaborators believe that the contraction of this muscle dilates the cavity of the atrium and at the same time probably closes the ostium; 'this causes the inspired air to filter through the 'external pores of the superficial layer'. They consider that the expulsion of the air is brought about by the contraction of the dorso-ventral body muscles, which express the contained air through the spiracle; the air is drawn into the tracheal tubes when the action of the muscles ceases.

In her account of the spiracle of *Ixodes ricinus*, Samson describes a valve-like structure which she considers is brought into play in order to prevent the air from entering the atrium; ticks, it should be noted, may remain a long time under water without being drowned. Opening into the atrium there is a bent tube, the dorsal wall of which is formed by a rigid chitinous plate, while the ventral wall is folded and consists of elastic chitin. The tube leads into the main tracheal trunks and has attached to its ventral wall just below the folded portion a row of chitinised teeth which are not unlike similar structures found at the entrance of the tracheae of other arthropods.

The tracheae

On the internal surface of the spiracle a number of large tracheal trunks are seen to emerge from it and to pass inwards; they may be conveniently divided into anterior, median and posterior sets. The anterior trunk passes forwards along the ventral surface close to the salivary gland; it gives off numerous fine branches for the skin, legs and other adjacent structures. About mid-way in its course a large branch is given off for the supply of the salivary gland, and from this a smaller branch goes to the brain. Near its anterior end a large branch is given off for the supply of the mouth parts, salivary ducts, etc.; this branch in many cases joins its fellow of the opposite side and forms the so-called ‘tracheal plexus’, situated near the brain. At its termination the main anterior trunk gives off a large external branch which divides into two or more branches for the supply of the coxal gland, skin, legs, Gene’s organ, etc. The main middle trunk soon splits into two secondary branches; the anterior of these supplies the dorsal skin, the lateral diverticula, the mid-intestine, the Malpighian tube, oviduct, etc. The posterior branch is almost entirely restricted to the ovary and oviduct. The main posterior trunk also divides into two branches, the anterior of which supplies the ovary and connected structures; the posterior branch goes to the posterior diverticula, rectum, Malpighian tubes, etc.

The heart and vessels

The *heart* is situated in the middle dorsal line, immediately below the integument and about the level of the stigmal plate. It lies on the mid-intestine, and can often be seen pulsating, through the integument, in nymphs. It is oval in shape, and is produced into two pouches at its posterior end. On the ventral surface there are two pairs of slit-like openings (ostia), leading into channels which extend up to the dorsal wall. The aorta commences at the anterior end of the heart, and passes forwards in close apposition to the mid-intestine. At its anterior end it expands into a sinus which surrounds the oesophagus and brain, the ventral surface of the sinus becoming fused with the ventral body wall, and the dorsal wall with the sheaths of the mandibles. There are in addition four pairs of lateral vessels which pass into the legs. The course of the circulation is the same as that in the Insecta; the blood from the body cavity is drawn through the ostia into the chamber of the heart and is propelled forwards along the aorta and lateral vessels.

The Nervous System

In proportion to the size of the animal the nervous system of the tick is very small. It consists of a single ganglionic mass (Plate LXXXIII, fig. 1), representing the fused ganglia and termed the *brain.* This structure lies in the triangular space anterior to the mid-intestine, superficial to the vagina in the female and to the 'white gland' in the male. It is traversed by the oesophagus in the usual manner. Branches are given off directly for the supply of the legs and the internal organs. On section it is seen to consist of an outer zone of nerve cells and an inner non-medullated zone.

Connective tissue and fat body

Ticks do not possess a large amount of connective tissue; there are, however, a number of loose strands connected by tracheae, which form a cellular matrix to support the organs; in stained specimens small nuclei may be seen lying on the strands. In the nymph and the adult there are in addition many large single cells, especially marked just below the skin and along the main tracheae, which appear to be true fat body cells. In the egg-depositing female these increase in size and later undergo a fatty change, their protoplasm becoming filled with clear droplets; in the Ixodini they are very conspicuous and may be mistaken for parasites.

The Integument

The integument of a tick, is of a leathery character. In the Ixodini it is formed of a semi-transparent, smooth layer of chitin which is hardened in certain parts to form rigid plates and shields, such as the scutum, anal plates, etc. In the Argatini, on the other hand, the integument may be either adorned with discs which are arranged in radiating lines and which serve for the attachment of muscles, or it may have mammillae giving it a granular appearance; there are no shields or plates of hardened chitin. On section the skin is seen to be composed of two layers, an outer chitinous and an inner cellular layer. The chitinous layer varies in thickness, and in the unfed condition is indented by furrows which give it a serrated appearance on section; the external portion, therefore, appears to be more rigid than the internal, which is elastic and does not become folded. In the full-fed tick the chitinous layer is almost smooth and is thicker than in the starving condition. The cellular layer is formed of cells which vary in shape according to the condition of the animal. In the unfed state they are columnar in shape, while in the fed tick they are cubical. Their protoplasm is finely granular and stains very readily with haematoxylin; the nuclei are situated near the basal end and are round or oval in shape. The hairs which pierce the skin are distributed somewhat irregularly over the body, and lie in cups just below the surface; the cups are continuous with small canals which pass through the chitinous layer to the cellular.

The Muscular System

The inner surface of the integument serves for the attachment of muscles, which are arranged in groups and which divide the haematocoele into several compartments; the most prominent are those which run across the body from the dorsal to the ventral surface. One set arises from the scutum on each side of the middle line and passes downwards and backwards to be inserted on the ventral integument; another set arises on each side at the junction of the middle and posterior thirds of the body and passes downwards to the region of the anus. The origins and insertions of these muscles in the integument produce the characteristic furrows seen on the outer surface. A large band of muscles arises from the ventral surface of the scutum and from the integument in the neighbourhood of the fourth pair of legs and passes forwards and upwards to be inserted into the bulbs of the mandibles; these are evidently the retractors of the mandibles. Another set passes from the under surface of the capitulum and is inserted into the bulbs of the mandibles; these by pulling on the mandibles would protract them. There are also other bands of muscles which pass from the scutum to the mouth ring and are probably brought into play in tilting the mouth parts, a movement which is seen during the act of feeding, and also when the female is about to oviposit.

The Reproductive System. The female organs in the unimpregnated condition. Plates LXXXIII and LXXXIV

In considering the structure of the female reproductive organs it is necessary to describe first their appearance in the unfed, unimpregnated female, for the conditions change when the female attaches itself to the host and is impregnated. The *ovary*, which is quite unlike that of the Insecta, is a single hollow organ, and lies in a somewhat oblique direction across the body, behind the end of the mid-intestine and above the posterior diverticula. Its dorsal surface is in close contact with connective tissue, fat body, loops of Malpighian tubes and the posterior part of the heart. In the Argatini the ovary is short and broad, while in the Ixodini it is U-shaped (Plate LXXXIV, figs. 2 and 5), and is often extremely long and narrow, filling up the posterior part of the body. In the unimpregnated condition it consists of unripe ova which may be recognized by their shining brown appearance; each ovum contains a large quantity of yelk and is loosely attached to a delicate membrane. The ova appear to be formed only on the dorsal area of the ovary, and are of varying sizes and arranged in regular rows; the ventral portion consists almost entirely of the delicate membrane and has no germ cells.

Oviduct, uterus and vagina

Each end of the ovary becomes continuous with a long coiled tube, the *oviduct*, which passes forwards and upwards to form one or more loops, and ends by uniting with its fellow of the opposite side to form a large sac-like organ, the uterus; at the point where the oviduct joins the ovary the former consists of a delicate membrane and is easily torn. The oviduct is lined by columnar cells which have large basally placed nuclei; external to the cellular layer there are some delicate muscular fibres which are strongly developed in the impregnated female. The oviduct has several dilated portions, very conspicuous in *O. savignyi*, the nature of which is not clearly understood. The *uterus*, which is also spoken of as the spermatheca, is a bicornuate organ formed by the junction of the two oviducts; it lies in the middle line below the mid-intestine. Its structure is very similar to that of the oviduct, and in the unimpregnated condition the circular muscle fibres surrounding it are not well developed. At its anterior end it becomes continuous with the *vagina*, a short tube which for purposes of description may be considered in three parts. The first part extends up to the entry of the vaginal glands; this portion is lined by flat cells covered by a delicate epithelial intima, and the muscles surrounding it are poorly developed in the unimpregnated condition. The *vaginal* or *accessory glands* are long sausage-shaped organs which open on each side of the first part of the vagina; they are similar in structure to the mucus accessory glands of insects. The glands are not present in *O. savignyi*, but are well developed in *Argas persicus* and in the *Ixodini*. The second part of the vagina is short, and has numerous papillae on its internal surface; even in the unimpregnated condition it is surrounded by a thick layer of circular muscle fibres. Inserted into its external walls on each side there are strong bands of muscles which arise from the dorsal integument; these draw it towards the dorsal surface. The third part of the vagina is usually named the *vestibule*; it leads directly to the external genital opening and is in close contact with the ventral surface of the brain. In structure it is very similar to the second portion, but the chitinous intima is better developed.

In the impregnated condition the ovary is seen to be increased in size and to contain eggs at all stages of development; these soon begin to project from the surface and are easily dislodged. When the egg attains maturity it is attached by a funnel-shaped neck, the *funicle*, which consists for the most part of flattened cells of the membraneous wall of the ovary. Further growth results in the egg being liberated into the lumen of the ovary; it is not very clear how this takes place, but it is probable that the neck of the funicle is forced open.

The organs in the impregnated condition

The mature egg is globular in shape and of a brown colour; its cytoplasm is packed with granules, so that the nucleus is not visible. The eggs pass from the oviducts to the uterus and from there into the vagina, from which they are finally expelled in a manner which will be described presently.

The circular muscle fibres of the oviducts and uterus are much better developed, and the former stand out as thick white cords. The muscle fibres of the vagina also increase enormously and the strands from these pass inwards to the cells lining the lumen. These, instead of being flat as in the unimpregnated condition, are now cylindrical, and as a result the lumen has become narrowed.

The vaginal glands, which in the unimpregnated condition were undeveloped, now take on their function. The cells lining the lumen are small and columnar in shape and have large nuclei; clear drops of secretion collect around the nucleus until the cells become almost completely filled with it. This secretion probably aids in the passage of the egg from the first part of the vagina into the vestibule.

Oviposition

Egg laying begins at a varying period after the female leaves the host. Some time before the eggs are deposited the capitulum is pressed down till it comes to lie at right angles to the body and is almost in apposition with the external genital opening. Gene's organ is now protruded (Argatini) until it projects over the capitulum; the vestibule is everted by the action of a complicated musculature and the palps are directed outwards. An egg is now extruded and rolled round until it comes in contact with the sticky secretion of Gene's organ; when this takes place the organ is withdrawn and the egg is carried on to the dorsal surface of the tick. This explains how eggs which come out of a ventral opening are always found lying over the anterior end of the female.

The male organs: The testis

The *testis* of the tick (Plate LXXXVI, fig. 5) is a delicate transparent tube, lying in the position occupied by the ovary in the female. Along its course there are many cystic swellings, which give it an irregular outline. The distal end on each side becomes continuous with the vas deferens, there being no distinct line of demarcation between them. The greater part of the

PLATE. LXXXVI.

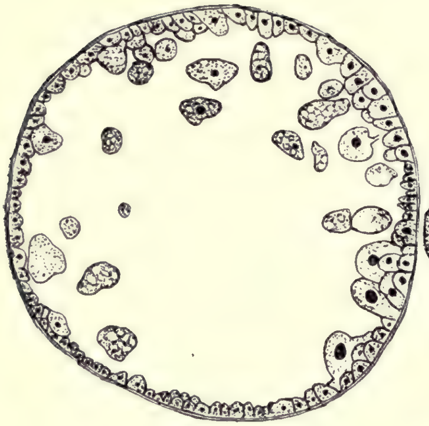

Fig. 1.

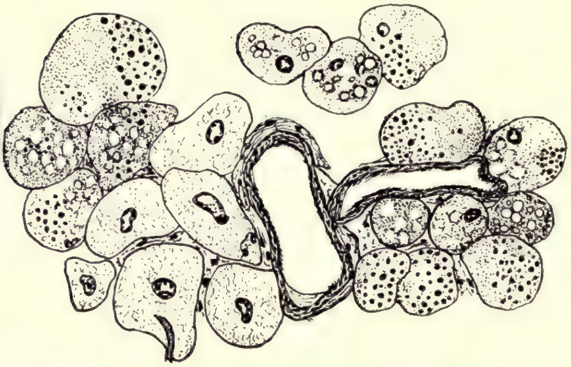

Fig. 2.

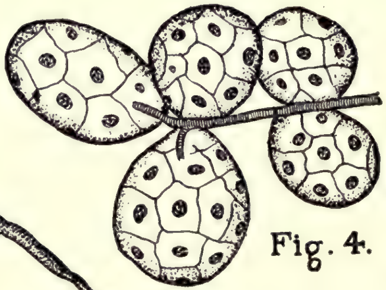

Fig. 4.

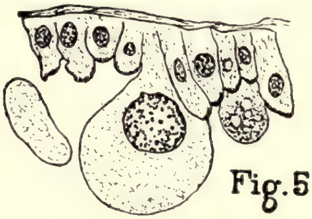

Fig. 5.

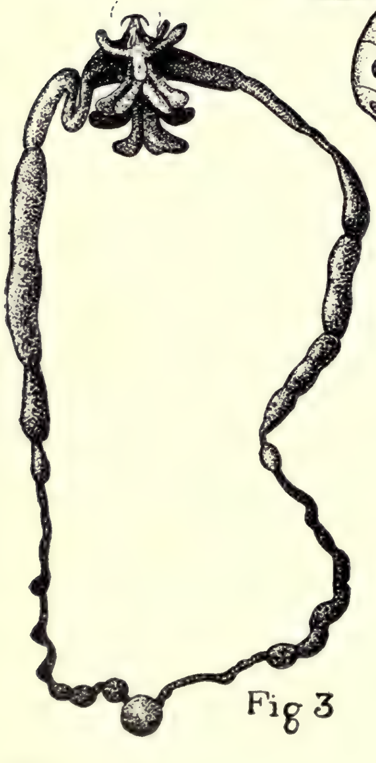

Fig 3

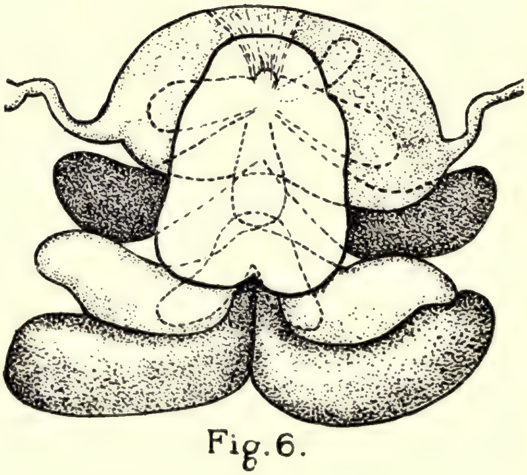

Fig. 6.

PLATE LXXXVI

Figure 1. Transverse section through an intestinal diverticulum of *Argas persicus*, in a late stage of digestion.

Figure 2. Transverse section through the salivary gland of *Argas persicus*, ♀, showing the different types of cells.

Figure 3. Genital organs of *Argas persicus*, ♂.

Figure 4. Salivary duct and lobules of *Hyalomma aegyptium*, ♀.

Figure 5. Section through a diverticulum of *Argas persicus*, showing a small portion enlarged. Note the large cell being extruded, and the smaller cells ready to replace it,

Figure 6. White gland of *Argas persicus*, ♂.

PLATE LXXXVI.

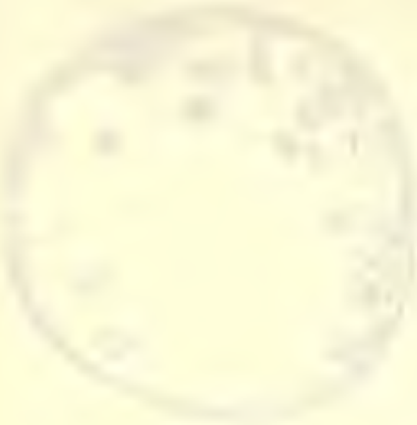

Fig. 1.

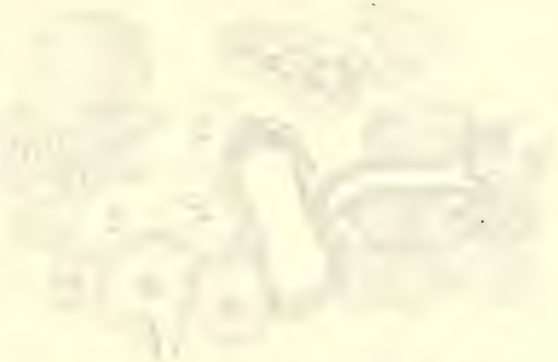

Fig. 2.

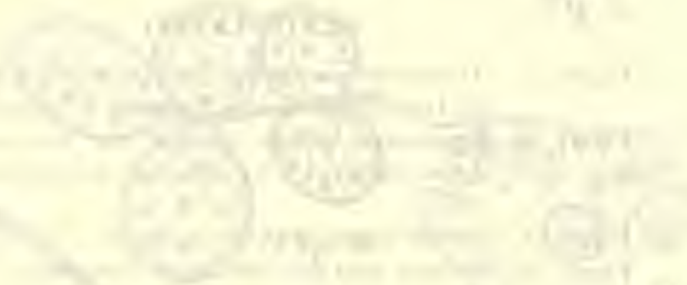

Fig. [illegible]

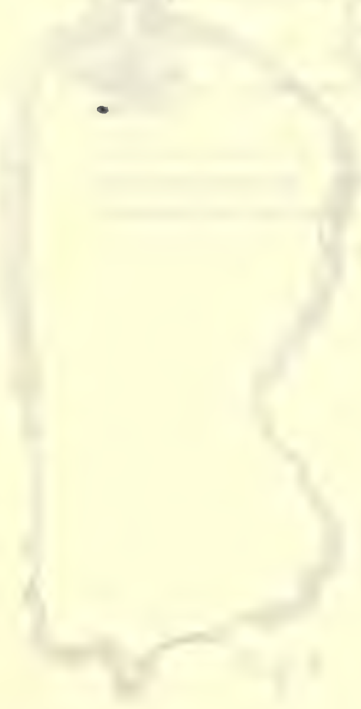

Fig. [illegible]

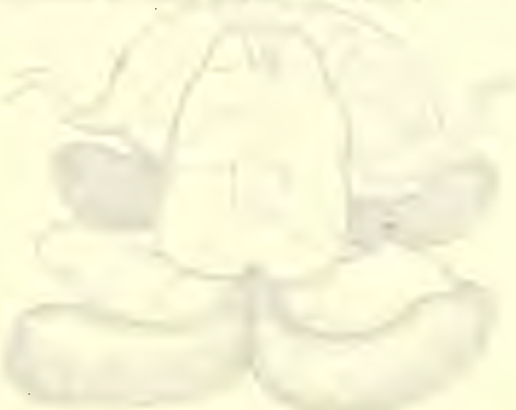

Fig. [illegible]

tube in the mature male contains formed spermatozoa, which, however, are not active and do not become so until transferred to the female. For an account of the mode of formation of the spermatozoa, which is very complex, and of their structure, the reader is referred to Samson's paper.

After making several coils the vasa unite in the middle line and there form a large lobulated organ, termed by Christophers the *white gland* (Plate LXXXVI, fig. 6). The terminal portions of the vasa are usually distended by large accumulations of spermatozoa and are easily ruptured. The white gland, which appears to function as a seminal vesicle, is lined by a single layer of high columnar cells. The accessory glands which open into it appear to play some part in the elaboration of the spermatophore. The number of such glands varies in different ticks; in *Argas persicus*, for instance, there are five pairs (fig. 6).

Spermatophore

The *spermatophore* consists of a coiled ball of sperms surrounded by a delicate membrane, external to which there is a tougher membrane which appears to be formed from the secretion of one of the accessory glands. The shape of the mass varies; in *Ixodes ricinus*, according to Samson, it is round, while in *Ornithodorus* it is flask-shaped with an opening at the end of the flask. The spermatozoa pass out of the spermatophore and make their way into the oviducts, where fertilization appears to take place.

Copulation

The act of copulation in ticks is unlike the corresponding one in insects. It is best studied in the Argatini, which leave the host after each feed. If bred males and females are kept apart until after the first feed, and then placed together in a petri dish, the act usually takes place at once. The male exhibits great activity on first meeting the female, crawling rapidly and repeatedly over her body and finally passing below her in such a way that the ventral surfaces of the pair are in contact with one another. The male then clasps the female in a characteristic manner, each pair of his legs being in advance of the corresponding pair of the female. The mouth parts of the male take the place of external genital organs—for it will be noted that the male has no such structures—and these are passed over the ventral surface of the female until the genital orifice is found; they are then inserted and withdrawn several times, apparently with the object of dilating it. They are then finally withdrawn as the male passes a little forwards until his genital orifice is opposite that of the female. A spermatophore is now rapidly ejected and applied to the lip of the orifice, and pushed in by the mandibles and hypostome. The male then abandons the female. If ticks are separated at the appropriate moment the spermatophore, a delicate and transparent flask-shaped bag of sperms, can be seen attached to the vulval orifice. After the act the ventral surfaces of both male and female are bathed in a clear fluid, the excretion of the coxal glands. The act of copulation is carried out in the same way in ***Argas persicus***, ***Argas vespertilionis***, ***Aponomma gervaisi*** and a number of others in which it has been observed.

Parthenogenesis in ticks

In a recent paper Aragao has described parthenogenetic reproduction in a species of ***Amblyomma***, ***A. agamum***, from Brazil; he was able to raise this tick through three generations in the complete absence of the male. This appears to be the first time that this phenomenon has been observed in ticks. Nuttall has since been able to show that parthenogenesis occurs in ***Rhipicephalus bursa***, the sheep tick of Southern Europe and North Africa; in this case, however, the male is well known. Nuttall found that if females were placed alone upon a sheep they remained on it from twenty-five to thirty-eight days and then abandoned the host without having become full-fed; some of these females began to oviposit after the normal interval and although many of the eggs shrivelled, larvae hatched from a few of them.

COLLECTION AND PRESERVATION OF TICKS

Where to look for ticks

In tropical countries almost all animals, both domestic and wild, harbour ticks, though some are more infested than others. In most cases the immature stages are found on the same host as the adults, but, as has been already pointed out, the larvae and nymphs of some ticks do not feed on the same species as the adults, so that it does not necessarily follow that the young stages occurring with adults belong to the same species. In searching animals for ticks every part should be carefully examined or they may be overlooked. Larger animals should be thrown and examined all over, particular attention being paid to the abdomen, the udder, and the scrotum; some ticks attach themselves about the anus. The eyelids and ears, especially inside the concha and along the margin of the latter, should be carefully examined; the ear is a favourite site for *Haemaphysalis*. The root of the neck and the tail should also be particularly examined.

In the case of canines, such as the dog, fox and jackal, particular attention should be paid to the ears and feet, and especially to the spaces between the toes; rhipicephalines are very fond of crawling deep down into the ear and burying themselves out of sight. In the jackal these ticks also attach themselves under the long hairs on the neck; they can often be located by passing the hand over the skin.

The ticks (*Haemaphysalis*) which are found on cats always select the ears, to the margins of which they attach themselves; the same is true of the mongoose, squirrel, rat, mouse, shrew and similar small animals which harbour ticks of this genus. In the case of squirrels and rats the ticks often select the root of the tail and the adjacent portion of the back.

The ticks of birds usually select parts which are devoid of feathers, such as under the wing, around the eyes, parts of the neck, etc.; the feet, especially between the toes, are also favourite sites.

Method of removing ticks from the host

Ticks should be detached from their host with great care, to avoid breaking off the mouth parts. The most satisfactory method is as follows:—Grasp the body of the tick between the thumb and forefinger, and depress the latter so as to get the nail just over the capitulum. By exerting slight pressure the body of the tick is made to act as a wedge, and in most cases it will relax its hold on the skin. When the tick is very deeply embedded, as in the case of *Hyalomma aegyptium* and *Amblyomma hebraeum*, forceps may be used, but they should be avoided as far as possible, as they are apt to damage the specimen by tearing off the legs if they slip. Force must on no account be resorted to, or the mandibles or hypostome will be torn off. A drop or two of zylol often causes the tick to withdraw its mouth parts, but in the case of *Hyalomma aegyptium*, where the entire capitulum is buried in the skin, even this procedure fails. Repeated attempts should be made with the thumb and forefinger and with a little patience in most cases the tick comes away. When ticks are removed from their hosts a ring of skin comes away with the mouth parts; it can be removed later, when the specimen is hardened, with a pair of forceps. Larvae and nymphs are as a rule easy to dislodge. If a female is nearing repletion it should be allowed to become full-fed, when it will drop off of its own accord.

The male tick is often found lying below the female, to which it clings, seldom having its mouth parts in the skin of the host; it comes away with the female.

Preparation of permanent specimens

The most successful way of preparing ticks for examination is that employed by Christophers. The specimen, preferably not replete, is placed between two glass slides, which are held in position by rubber bands made by cutting off pieces of ordinary rubber gas tubing; string will do equally well.

The pressure causes the tick to spread out its legs, thus preventing them from obscuring the view, as they do when curled up; in many cases the palps are separated, permitting a better view of the mandibles and hypostome. To fix the tick in this position the slides are dropped into boiling water or boiling seventy per cent alcohol, which kills it instantly and without any alteration in position. The slides are placed in cold seventy per cent alcohol in suitable glass tubes for twenty-four hours, and the tick then removed; in some cases it is necessary to place the slides for a short time in absolute alcohol. The specimen is then transferred to a small tube in fresh seventy per cent alcohol, taking care to have a good cork.

Making of cleared specimens

Ticks can be cleared by placing them in a two per cent solution of caustic potash in the cold; the solution should be filtered before use and changed after forty-eight hours. A small nick should invariably be made in the body in some unimportant site so as to allow the potash to penetrate into the interior. After the tick has been in the solution for four days it should be gently compressed with a flat pair of forceps, when the dissolved internal organs will exude as a yellow fluid. When the specimen is sufficiently cleared—this can only be learned by experience—it should be washed in running water for ten minutes, and then dehydrated by passing it through graded alcohols up to absolute alcohol; it should then be cleared in oil of cloves for several hours and mounted in canada balsam. If necessary, the integument and other parts can be stained with a saturated solution of carbol fuschine or Orange G, after washing and before dehydration. The specimen may be mounted in any desired position either on a plane or in a hollow slide. Larvae and nymphs should be treated in the same way. Eggs may be preserved in the way described for the eggs of Diptera (see page 417).

Special structures may be mounted separately, after dissecting them out while the tick is soft or when it is in the oil of cloves. In this way the capitulum, the mandibles, hypostome, palps, legs, and spiracle may be removed; they make excellent mounted specimens.

Keeping of live ticks

Ticks required for further experiment may be kept alive as follows:—Place them as they drop off the host in ordinary test tubes, the mouths of which are plugged with cotton surrounded by thin paper—the paper prevents larvae from becoming entangled in the wool. The tubes should be placed on their sides on a cupboard, each with a label which corresponds with the entry in the notebook in which all the details regarding each specimen are written.

About a dozen or more larvae may be kept in each tube. In some cases it may be necessary to keep the ticks in a moist atmosphere; in this case they should be placed in pill boxes kept in moist sand. This is very necessary in the case of certain species of *Aponomma*, or the eggs often fail to hatch; it is best to allow them to oviposit in sand.

Ticks should never be placed in corked tubes or they will bury themselves in the cork, or between the glass and the cork; this is specially likely to happen in the case of larvae.

Ticks for identification should be sent either to Professor Neumann or Professor Nuttall, whose addresses are given below. The specimens should be placed in seventy per cent alcohol, and a label giving details of host, locality, etc., written in pencil placed inside the tube.

Professor L. G. NEUMANN,
École Nationale Vétérinaire,
Toulouse,
France.

Professor GEORGE H. F. NUTTALL, F.R.S.,
Quick Laboratory,
Cambridge,
England.

LITERATURE

As a complete Bibliography (see below) on ticks has recently (July, 1911) been published by Nuttall and his co-workers, only references to papers and monographs which the authors have found useful in the preparation of this chapter are given below; for references to the other works dealing with ticks the worker should consult Nuttall's Bibliography. The worker should consult also the recent volumes of *Parasitology*, which contain numerous papers on ticks:—

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Donitz, W. — Die wirtschaftlich wichtigen Zecken mit besonderer Berücksichtigung Afrikas. 1907. J. A. Barth. Leipzig.

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Idem — Tick Heartwater Experiments. *Report of the Government Entomologist*, for the year 1900. Tick Heartwater investigations—Tick Malignant Jaundice investigations. *Ibid.* 1901.

Idem — Ticks and Rhodesian cattle Fever—Ticks and Malignant Jaundice—Ticks and Heartwater. *Report of the Government Entomologist*, 1902. The fowl tick. Studies on its life cycle and habits. *Agricult. Journ*, Transvaal. 1903. Transmission of African Coast Fever. *Ibid.* xxiv, 1904.

Idem — Habits and peculiarities of some South African Ticks. *British Assoc. for the Adv. Sc.*, Section D. South Africa, 1905.

	All the above papers and many others not listed, contain valuable information on the life histories and habits of South African Ticks.
Hooker, W. A., Bishopp, F. C., and Wood, H. P.	The Life History and Bionomics of some North American Ticks. *U. S. Dept. of Agriculture, Bureau of Entomology, Bull.* No. 106, 1912. Contains very full information regarding most of the North American ticks, together with excellent photos.
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CHAPTER IX

THE ORDER ACARINA: MITES

THE term mite is conveniently, though somewhat loosely, applied to a large assemblage of acari, mostly of small, often minute, size, contained in the order Acarina, the family Ixodidae being excluded. Mites are widely distributed in nature and are both terrestial and aquatic in habit; the species are most numerous in temperate zones and may be found at great altitudes. The majority are free-living; a few, however, are parasitic and are found on a great variety of hosts, including mammals, birds and insects; some species are parasitic in their immature stages and free-living in their adult stages, and a few utilize insects as a mode of transport from one breeding ground to another. With the exception of the Ixodidae, the acari have attracted very little attention from naturalists, and detailed information, especially with regard to their biology, is very scanty.

Relation to disease

Many of the Gamasidae are true blood-suckers, and have habits similar to those of the ticks, to which they are closely related. They may therefore act as the transmitters of blood parasites, and one instance of this is known, that of the transmission of *Leucocytogregarina muris* by *Laelaps echidninus.* Among the Trombidiidae there are several imperfectly differentiated species which cause skin eruptions at certain seasons in those exposed to their bites. The family Sarcoptidae includes the mites which cause scabies in man and corresponding diseases of the skin of animals, while *Demodex folliculorum,* a vermiform acarian, which lives in the sebaceous glands and hair follicles of man, is believed by Borrel, though on somewhat slender evidence, to be associated with the spread of cancer and leprosy. A species of *Trombidium, T. akamushi,* Brumpt, is said to be associated with the disease known as Japanese River Fever or 'Tsutsugamushi' disease. People who handle cereals are sometimes affected by an eruption due to a species of *Pediculoides* which lives in the grain.

FAMILY GAMASIDAE

Body flat and broad, and furnished with plates and shields as follows:— A pair of plates, the jugularia, just behind coxa I on the ventral surface;

a pair just behind coxa IV, the metapodia; a third pair, the metasternalia, behind the sternal plate; these plates may be differently arranged in the two sexes, and are fused together in the male. The female genital opening is usually under the margin of the genital plate, which terminates near coxa III, that of the male just behind the mouth parts, at the anterior margin of the sternal plate. Anal plates usually present. Anal opening as a rule small and situated at or near the posterior margin of the ventral surface, which is smooth and devoid of furrows; posterior margin not crenulated or festooned. Stigmata between legs III and IV; the peritreme usually well developed. Eyes absent. Mouth parts formed for piercing; the hypostome, unlike that of ticks, smooth and not armed with teeth. Legs of the usual arthropod type; the second pair in the male in many of the species armed with teeth used in clasping the female.

The members of the Gamasidae, also known as the Parasitidae or Insect mites, exhibit great diversity in habits. The majority are vegetable feeders, some being injurious to cultivated plants, while others are found among decaying leaves and other vegetable debris. A considerable number are predaceous; others are true blood-suckers, living on the blood of small rodents, bats and birds. As these latter are the most important from our present point of view it will be convenient to take one of them as an example for descriptive purposes. *Laelaps*, a species of which from the Indian field rat, *Gerbillus indicus*, is figured on Plate LXXXVII, will serve for the purpose.

External anatomy of Laelaps: The Mouth Parts. Plate LXXXIX, figs. 1, 2 and 3

The body is built on the same general plan as that of a tick. The head and thorax are fused together to form the *cephalothorax*, which in this species is oval, though various shapes are met with in other forms. The *capitulum* projects a little from the anterior end of the body and bears the mouth parts, including the maxillary palps. The mouth parts consist of paired mandibles, maxillae and a median hypostome. Each *mandible* is an elongated rod of chitin consisting of two segments, of which the distal one is the longest. The appendage differs in the two sexes. In the female it terminates in a pair of digits which are articulated to the end of the mandible and oppose one another like the claws of a crab; each digit is cone-shaped, and is armed with three or more strong teeth, while a long thin hair ending in a hook arises from the median surface of the external digit. Attached to the base of the mandible there is a row of hairs arranged in a fan-like manner, those on the outer side being longer than the rest. In the male the mandibles are highly modified and are armed with structures believed

PLATE LXXXVII

Figure 1. *Laelaps sp.*, from *Gerbillus indicus*. an.d., anterior diverticulum. ca., capitulum. cl., claws. F. Femur. hy., hypostome. md., mandibles. md.i., mid-intestine. p., palps. pl., pulvillum. pt.d., posterior diverticulum. psa., pseudo-articulation. pts., protarsus. sc., scutum. ts., tarsus. tr., trochanter. × 60.

Figure 2. Claws and pulvillum of first leg of same.

Figure 3. Claws and pulvillum of second leg of same.

Figure 4. Leg of *Pteroptus vespertilionis*.

Figure 5. *Pteroptus vespertilionis*, ♀. an., anus. a.p., anal plate. cl., claws. cx., coxa. emb., embryo. F., femur. g.p., genital plate. hy., hypostome. p., palps. pl., pulvillum. p., peritreme. pts., protarsus. sp., spiracle. st.p., sternal plate. tb., tibia. tr., trochanter, ts., tarsus. × 50.

PLATE.LXXXVII.

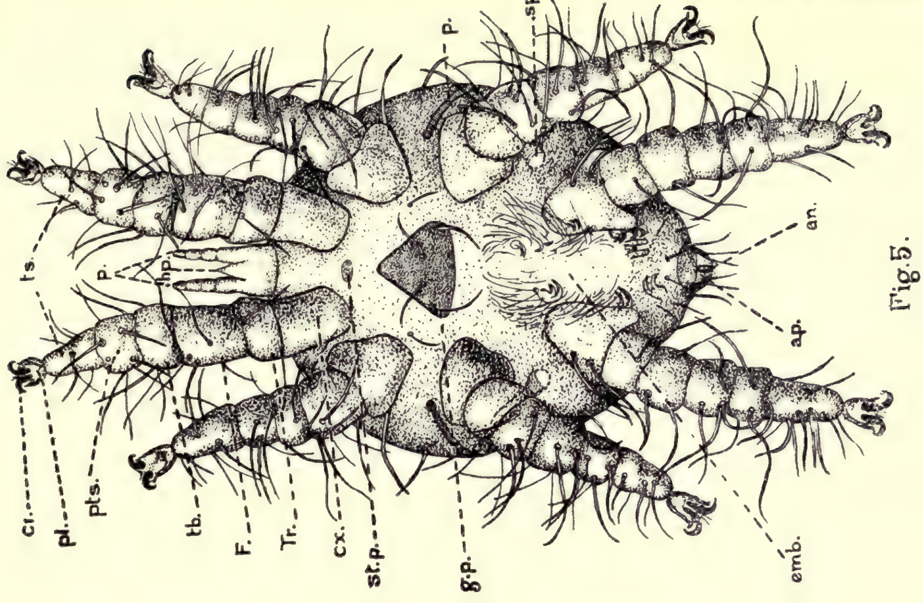
p.
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Fig.5.

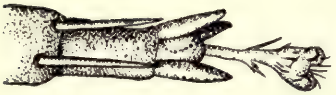


Fig.3.

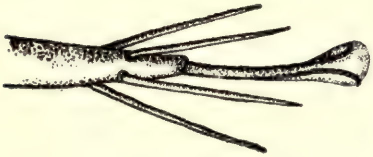


Fig.2.

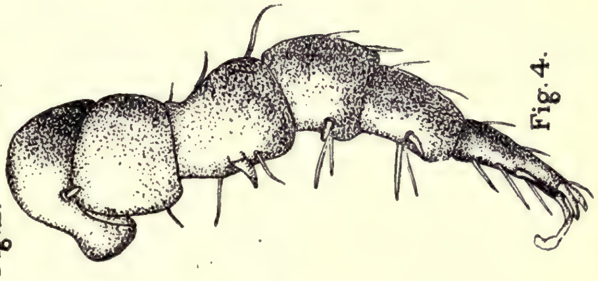
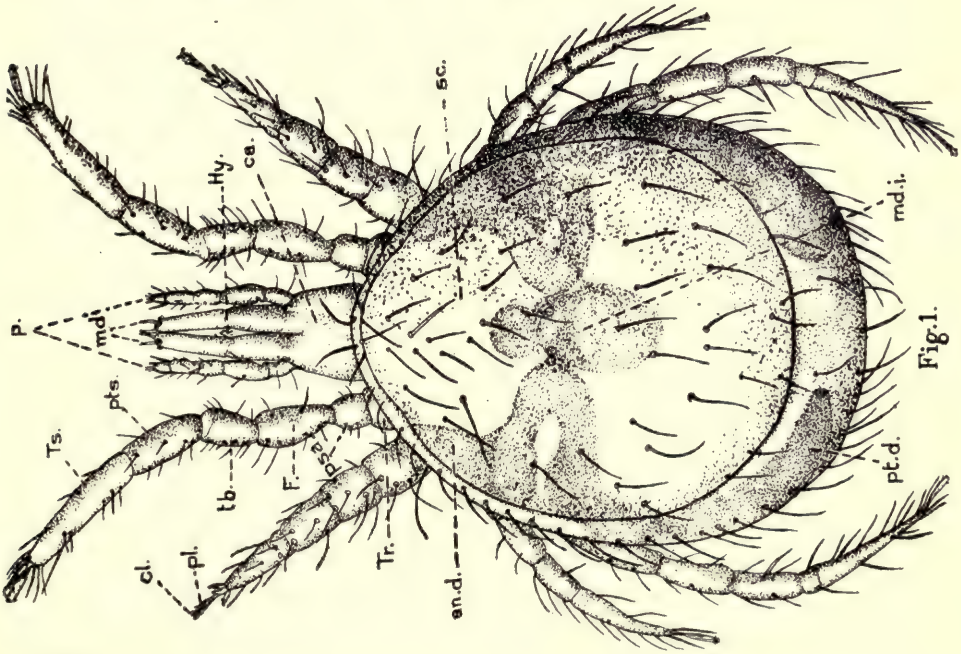


Fig.4.


sc.
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ca.
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md.j.
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Ts.
tb.
F.
psa.
Tr.
cl.
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an.d.
pt.d.

Fig.1.

to be of a sexual nature; the appendage is shorter and broader than that of the female, and in place of the external digit there is a long blade-like slip of chitin with a delicate hooked hair on its inner side; in place of the internal digit there are two rod-like pieces of chitin, one of which is hooked at its end like a shepherd's crook. Attached to the ventral side of the end of the mandible there is a club-shaped pad, directed inwards towards its fellow of the opposite side, and with a fringe of delicate hairs along its margin.

The *maxillae* are situated at each side of the buccal cavity, above the lateral arms of the hypostome, and are much smaller than the mandibles. Each is a flat and narrow blade of chitin, ending in a sharp point and evidently intended for piercing. The hypostome is situated on the ventral side, and is spatulate and divided into a central cone-shaped portion and two lateral arms, which lie just below the maxillae. The hypostome is not armed with recurved fixing teeth, and therefore probably does not fulfil the same function as in the ticks. As all blood-sucking gamasids are intermittent feeders the hypostome, like that of the Argatini, is only used as a cutting weapon.

The food canal is formed by the apposition of the hypostome and mandibles above and the maxillae below, the sides being closed in by loose folds of the lateral integument.

The palps

The palps are filiform, and consist of five short segments, the terminal one of which is armed at its apex with a number of sensory hairs, grouped together as in the ticks. On the inner side of the fourth segment and just below its apex there is a large curved spine, shorter and stouter in the male than in the female; and in the same situation in both sexes there is a pair of peculiar short spines with globular ends. The second segment has a long spine on its internal border.

Structure of body: scutum, stigmata and plates

The cephalothorax is covered dorsally by the *scutum*, which in the female almost completely conceals it; the scutum is seldom marked with spots and colour designs. The stigmata are situated in the usual position behind and external to coxa IV; the peritreme is well developed and extends forwards to the dorsal surface. The ventral surface is provided with shields very much as in the ticks; there is a sternal plate as well as genital and anal plates; in some mites in addition there are one or more small accessory plates. The female genital opening is situated between the sternal and genital plates, the male opening on or near the sternal plate. The anal opening lies on the anal plate and often has a large spine on its posterior margin.

The Legs

The legs are well developed and consist of six segments resembling those of ticks; the number of segments may, however, be considerably reduced in some of the parasitic forms. The tarsus in *Laelaps* has peculiar spines at its apex, which, together with the short or long spines on the segments of the legs, are of value in distinguishing the species.

Internal Anatomy of Laelaps

The *alimentary tract* is very similar to that of ticks, and when fully developed, as in a *Laelaps*, consists of the pharynx or pumping organ, the oesophagus, the mid-intestine with its diverticula, the hind-intestine, with the rectum and Malpighian tubes.

The Alimentary Tract

The *pharynx* or sucking pump is situated on the ventral surface of the capitulum, and consists of a straight or slightly bent tube formed of chitinous plates united to each other by a membrane. A series of muscles arise from the dorsal and lateral walls of the capitulum and are inserted into the walls of the pharynx above and at the sides; on contracting, these pull them apart and thus produce a negative pressure. In addition there are small circular fibres which surround the pharynx and interlace with each other; these muscles constrict the pharynx and thus aid in propelling the blood into the oesophagus.

At the posterior end the pharynx becomes continuous with the oesophagus, which is a slender tube lined with a delicate chitinous intima and surrounded by small bundles of circular muscular fibres. After a short course the oesophagus passes downwards and then upwards through the brain to enter the mid-intestine on its posterior surface. The *mid-intestine*, as in the ticks, lies in the middle line and is a short thin-walled sac. On each side it gives off a short diverticulum which divides into an anterior and posterior branch; the anterior branch passes forwards and ends in the neighbourhood of the mouth parts; the posterior branch meets its fellow of the opposite side and ends in the neighbourhood of the rectum. The mid-intestine and its diverticula are lined by a single layer of large columnar epithelial cells which rest on a basement membrane; external to this there is a series of fine parallel muscular fibres. During digestion the cells exhibit appearances similar to those which have already been described in the case of ticks.

Posteriorly the mid-intestine becomes continuous with the *hind-intestine*, which passes downwards and backwards to end in the rectum, and is not patent throughout its entire length. The *rectum* is a large sac with thin walls lying in the middle line; it is usually filled with a whitish fluid, the excretion of the Malpighian tubes. The tubes begin blindly in the neighbourhood of the mouth parts and pass backwards below the mid-intestine, to end on the posterior surface of the rectum; as in ticks they come in contact with most of the organs.

Hind-intestine, rectum and Malpighian tubes

The *salivary glands* lie on each side of the anterior end of the body; each gland is elongated and broadest at its posterior end. It consists of a number of acini lined by large granular cells, which form lobules; small ducts pass from the lobules and enter the main salivary duct, which enters the buccal cavity at its posterior end; accessory glands are also present.

Salivary Glands

In many of the aberrant forms some of the organs described above are not fully formed. The reproductive organs are very similar to those of ticks and do not call for any separate description.

The Gamasidae have been classified in many different ways by different authorities, and, as in the case of ticks, the tendency has been to raise them to the level of a superfamily, as the Gamasoidae (Banks), dividing this into several families. In the following the classification of Banks is followed, the group being however regarded as a family, and his families as subfamilies.

Subfamilies of Gamasoidae (after Banks)

1.	Parasitic on vertebrates; mandibles fitted for piercing; body sometimes constricted	**Dermanyssinae.**
	Free, or attached to insects (rarely on vertebrates, never on birds)	2
2.	First pair of legs within the same body opening (camerostoma) as the oral tube; dorsum of body projects beyond the camerostome; genital aperture surrounded by the sternum.	**Uropodinae.**
	First pair of legs inserted at one side of the mouth opening; dorsal surface of body does not project in front of the camerostome; male genital aperture usually on the anterior margin of sternal plate (sometimes in the middle)	**Gamasinae.**

SUBFAMILY DERMANYSSINAE

The distinctions between the Dermanyssinae and the Gamasinae are by no means well marked, as many of the forms are very similar in structure and merge into each other; most of the Dermanyssinae, however, are parasitic, and this seems to be the main distinction between the two subfamilies. Banks arranges the important genera as follows:—

BANK'S KEY TO THE GENERA OF DERMANYSSINAE

1.	Anal plate present	2
	Anal plate absent	5

2.	Body short; legs very stout, hind pair reaching much beyond the tip of body	**Pteroptus.**	
	Body longer; hind legs not reaching beyond tip of body		**3**
3.	Peritreme on the dorsum, very short; body very distinctly constricted	**Ptilonyssus.**	
	Peritreme on venter, longer; body not distinctly constricted		**4**
4.	Mandibles in both sexes chelate; parasitic on bats and mice	**Liponyssus.**	
	Mandibles in male chelate, in female long, styliform, parasitic on birds	**Dermanyssus.**	
5.	Dorsal shields present; coxae close together; living in seals.	**Halarachne.**	
	No dorsal shields; hind coxae separated from the fore; living in monkeys	**Pneumonyssus.**	

Genus Pteroptus, L.

The species belonging to this family are all parasitic on bats; they are remarkable on account of their curious shape. The abdomen is small and round in the female (Plate LXXXVII, fig. 4), and practically absent in the male. The legs, which are short and thick and covered with bristles, are inserted about equal distances apart around the body, so that the mite can walk forwards or sideways with equal facility, and often adopts a crab-like mode of progression. The stigmata are situated on the dorsum, but the peritreme extends round to the ventral surface as shown in the figure. The method of reproduction is peculiar; the eggs hatch out in the body of the female, and the larva is retained until the nymphal stage is reached. The nymph is just as active as the adult, and also lives on the wing of the bat. *Pteroptus vespertilionis* (Plate LXXXVII, fig. 4) is common on the yellow bat, *Scotophilus kuhli*, in Madras. Several allied genera have been described, but they probably represent immature stages of *Pteroptus*. All the species are blood-suckers.

Genus Dermanyssus, Duges

The species belonging to this genus are all parasitic on birds, the blood of which they suck; they may be recognized by the following characters:—The body is oval and soft and finely striated all over; the mandibles are different in the two sexes; in the female they form a long thin stylet, and in the male are chelate.

Dermanyssus gallinae, Redi, is the common and perhaps the only species; it is a temporary parasite of poultry, behaving in the same way as *Argas persicus*; the mites hide in cracks and crevices in the coops in the poultry yard, and especially in straw in pigeon coops, during the day, and come out at night to feed. Colonies, consisting of males, females and immature stages are found together in their hiding places. They occasionally attack man and may cause considerable cutaneous irritation.

The gamasids belonging to the genus *Ptilonyssus* are parasitic on passerine birds, and at least one species is found on the common sparrow; they are very similar to *Pteroptus,* but the abdomen is longer and is separated by a constriction from the cephalothorax. Several species of *Liponyssus* are known from mice and bats; they are very similar to *Dermanyssus,* but are of a lighter colour. The species belonging to the genera *Halarachne* are very little known; one species has been found in the bronchial passages of seals; it is elongated and looks like a miniature tick; the mandibles are divided pincer-fashion.

GENUS PNEUMONYSSUS

The mites of this genus are parasitic and blood-sucking, and inhabit the bronchi and lungs of monkeys. *Pneumonyssus simicola,* which appears to be the type species, was found in the lung of a Javanese monkey. Two new species, described in 1906 by Newstead, and placed in this genus, appear to differ considerably from the type, and it is possible that a new genus will have to be created for their reception. Both of these species possess a dorsal scutum, whereas the absence of this character is, according to Banks, the distinguishing feature between this genus and *Halarachne* (see above).

The following key will serve to distinguish the three species:—

1. Dorsal shield absent . . . . **simicola**.
   Dorsal shield present 2
2. Palp of three equal joints, the basal one twice as broad as the apical . . . . **duttoni**
   Palp four jointed, segments subequal . . . . . . **griffithi**

Pneumonyssus duttoni, Newstead, was found in the tracheae and bronchial passages of an African monkey, *Cercopithicus schmitdi,* in the Congo district. Only the adult females and the larvae were found, males being entirely absent. The females occur in the trachea and its first four or five subdivisions, the larvae mainly in the smaller bronchi. No symptoms are ascribed to their presence, except perhaps for a slight bronchitis. Eggs were not found.

Pneumonyssus griffithi, Newstead, is recorded from the lung of the Indian monkey, *Macacus rhesus.* Unlike the preceding species, it appears to produce definite pathological changes in the lung. In the infected animals—a series of six—the lungs showed numerous small cavities chiefly situated under the pleura, and varying in size from half to one millimetre in diameter. Each cavity is continuous with a small bronchus, and has a thin fibrous wall, lined internally by silvery white debris, in which the parasites are found. According to Griffiths, as quoted by Newstead, the majority of the monkeys examined were infected, the infection being more frequent and more intense in the older individuals. Acid fast bacilli—not the tubercle bacillus—were found in the debris in the cavities; whether there is any connection between the bacillus and the mite is not stated.

Probably there are many species as yet undescribed.

SUBFAMILY UROPODINAE

Most of the gamasids belonging to this subfamily are found on beetles and other insects. The mandibles are long and slender and end in pincers; in some species they are actually twice as long as the body of the mite. The species which are found on insects are not all true parasites; many attach themselves simply in order that they may be carried from one place to another. Such emigrant forms are nearly always nymphs, and are attached to their carrier by means of a long pedicel, said to be formed of the secretion of the glands in the region of the anus; they are known as *nympha pedunculata*. A few of the mites of this subfamily are true parasites, and live on ants. These parasitic forms never attach themselves by a pedicel.

SUBFAMILY GAMASINAE

This subfamily contains a large number of genera, many of the species of which are closely allied to the dermanyssids. Most of them are free-living, a few of the species are temporary parasites of mammals. Two closely allied genera contain several species which are parasites of rats and other small rodents, the blood of which they suck. Banks gives the following key to the two genera *Laelaps* and *Myonyssus*:—

Anal plate small, much smaller than the median plate . .	**Laelaps.**
Anal plate large, larger than the median plate	**Myonyssus.**

Genus Laelaps, Koch, C. L.

This genus contains a large number of species, among which there are a few which are parasites of rodents. The scutum is armed with many bristles and there are some on the margin of the ventral plates. There is also a bristle at the margin of the anal plate. Three species which are known from rats are distinguished by the following key given by Banks:—

1.	Dorsum with numerous fine hairs; no stout spines on coxae .	**stabularis.**
	Dorsum with fewer, but stouter spine-like bristles; each coxa has a stout spine	2

2. Body but little longer than broad; median plate longer than broad . . . . **agilis.**
Body much longer than broad; ventral plate about as broad as long . . . . **echidninus.**

Laelaps echidninus, Berlese. Dorsal surface of body almost completely covered by scutum and armed with rows of long curved bristles, six in front and eight behind; there is also a longer pair near the front margin and a few at the sides. The legs are stout and comparatively short; the tarsus is about twice as long as the preceding segment; there is a stout spine situated about the centre of each coxa.

This species is common on *Mus decumanus* and other rats in many parts of the world; according to Miller it is the invertebrate host of *Leucocytogregarina muris* in the United States.

Laelaps agilis has been recorded from rats in Europe and Africa, and *L. stabularis* is found on the brown rat in Italy. Doubtless there are many more species yet to be described.

The genus *Myonyssus,* Tiraboschi, contains one species, *decumani,* from Italy, where it has been recorded from *Mus decumanus.* The above key will help to distinguish it from *Laelaps.*

Two other genera, *Raillietia* and *Haemogamassus,* of which very little is known, are believed to be blood-sucking in habit. *Raillietia auris,* Leidy, occurs in the ears of cattle in the United States. The species belonging to *Haemogamassus* are found on moles in Europe and America.

FAMILY TROMBIDIIDAE

The mites of this family are characterized by the presence of an accessory finger-like appendage to the palps. The body is usually divided into two portions; the cephalothorax bears the anterior pairs of legs, the palps, mouth parts, and eyes; the abdomen proper is usually larger than the anterior part, and bears the two posterior legs. The last segment of leg IV is not swollen, while that of leg I is enlarged. Most of the species are of a red colour. Like the Gamasidae this family contains a number of forms with very varied habits. Those which come specially into prominence are the harvest mites, common in most countries and known by various local names, though the species have not as yet been properly differentiated on account of the difficulty of following the complete life history.

The adults of these harvest mites are mainly predaceous, but the larvae, which, as the name implies, appear in the autumn, are parasitic, and attack the skin of mammals and frequently of man. Their presence gives rise to considerable irritation and even vesication. It is a mite of this family which, in the larval stage, is believed to be the transmitting agent of Japanese River Fever.

Trombidium holosericeum, L., is the common European species, and is widely distributed. Recently Bruyant has pointed out that two distinct species have in the past been confused with *holosericeum*, namely, *T. rimosum*, Koch, and *T. latum*, Koch; they can be distinguished from one another by the character of the furrows on the cephalothorax and by the shape of the dorsal hairs.

FAMILY HYDRACHNIDAE

Body short and almost spherical, without any division into cephalothorax and abdomen. Legs arise close together and consist of seven segments. One or two eyes on each side of anterior end of body. Mouth parts not carried on a rostrum; suckers usually present near the genital openings. Living in fresh water.

This family contains the fresh water mites, several of the species of which, in their larval stages, are often found attached to the neck and abdomen of adult mosquitoes, particularly anophelines. They belong to the genus *Hydrachna*; their life histories are unknown.

FAMILY SARCOPTIDAE

Body as a rule soft; palpi small and three-jointed. Ventral suckers present at genital opening or near anal opening. Eyes wanting. Legs consisting of five segments; tarsi often end in suckers. Stigmata wanting. Adult often parasitic.

Banks, in his *Treatise on the Acarina*, places these mites in the superfamily Sarcoptoidea, which he divides into seven families. His superfamily is here retained as a family and the families as subfamilies. He gives the following key for their identification:—

BANKS' KEY TO THE SUBFAMILIES OF THE SARCOPTIDAE

1. With tracheae; no ventral suckers; legs ending in claws; body divided into cephalothorax and abdomen; the female with a clavate hair between legs I and II; not parasitic on birds or mammals . . . . **Tarsoneminae.**

Without tracheae; no such clavate hair 2

2. Genital suckers usually present; not parasitic on birds or mammals; skin usually without fine parallel lines 3

Genital suckers absent; parasitic on birds or mammals; skin with fine parallel lines 4

3.	Legs short, without clavate hair on tarsi I and II; living on insects	**Canestrininae.**
	Legs longer, with clavate hair on tarsi I and II; not parasitic except on bees	**Tyroglyphinae.**
4.	Possessing some specially developed apparatus for clinging to the hairs of mammals	**Listrophorinae.**
	Without such apparatus	**5**
5.	Living on the plumage of birds	**Analgesinae.**
	Not on plumage of birds, but in living tissues	**6**
6.	Vulva longitudinal; in skin and cellular tissues of birds	**Cytoleichinae.**
	Vulva transverse; in skin of mammals and birds	**Sarcoptinae.**

Only three of these, the Tarsoneminae, the Tyroglyphinae and the Sarcoptinae, which contain the itch mites, concern us here.

SUBFAMILY TARSONEMINAE

Soft bodied mites which resemble the Tyroglyphinae, *the female differing in having a club-shaped organ between legs I and II. Palpi minute and the mandibles slender and needle-like. The posterior pairs of legs are widely separated from the anterior. Legs short and composed of five or six segments; the anterior tarsi have one claw, the others two. Tracheae present, opening on the ventral surface near the base of the rostrum.*

This subfamily contains the genus *Pediculoides*, in which all the legs of the female end in claws and suckers. *P. ventricosus* is a common pest among those who handle cereals, and sometimes causes a cutaneous eruption.

SUBFAMILY TYROGLYPHINAE

Pale-coloured mites with soft bodies twice as long as broad and broadest just behind the middle. Mandibles chelate; palpi small. Legs long, ending in a single claw; the hair at the end of the penultimate segment of legs I and II is very long; a clavate hair near the bases of tarsi of legs I and II. Eyes and spiracles wanting. Genital orifice elongate and situated between the hind coxae.

The mites belonging to this family feed chiefly on vegetable matter, a few on animal substance as well; they are commonly found in cereals of all kinds, and in other products such as cheese, flour, ham, and dried meats; they often attack entomological specimens. A number of these mites have been known to attack man and to cause serious skin eruptions; Gedoelst gives the species which do so in his *Synopsis de Parasitologie.*

The life history of some of the tyroglyphid mites is very remarkable. Except for the species of one genus, which are viviparous, all lay eggs.

The larva is of the usual type, and after moulting is transformed into the typical arthropod nymph, which may now either become an adult or pass through another stage which is spoken of as the *hypopus*. The typical hypopus has no mouth parts and no distinct mouth orifice; its legs are short and not adapted for walking. It attaches itself, by means of a disc on the ventral surface near the apex of the body, to a flying or otherwise active insect, and is then transported to another locality. Arriving there it leaves its temporary host and carrier, and moults, the next instar being a typical nymph, which after feeding is transformed into an adult. Banks says that the causes which induce a nymph to become transformed into a hypopus are not known.

Glycyphagus domesticus, Gerv. Dorsal integument more or less granular; claws weak, almost invisible. Hairs of the body plainly feathered; anal and genital openings very large, the latter occupying the entire area between the coxae. This species lives in cereals and sometimes causes a transient cutaneous eruption in grocers.

Rhizoglyphus parasiticus, Dalgetty. Dorsal integument not granular; tarsi with stout spines. Leg I never thickened. This species causes the 'water itch' of Indian coolies in the tea plantations of Assam; it is at times a serious pest.

Tyroglyphus longior, variety *castellani*, Hirst. Dorsal integument not granular. Leg I of male not thickened. Palpi stout and appressed to rostrum. Suture between cephalothorax and abdomen very distinct. The variety differs from the type *longior* in minute details such as the absence of short hairs on the ventral surface of the body. It causes 'copra itch' in Ceylon. *T. longior* is common in Gorgonzola cheese.

SUBFAMILY SARCOPTINAE

The itch mites have long been known to entomologists. They burrow into the skin of man and many of the lower animals, including a few birds, and cause the diseased condition known as scabies (in man) and mange or acariasis (in animals). The mites are extremely small and of a white colour and globular shape; the integument is finely striated and is provided with a few bristles, which are often short and pointed. The legs are arranged in two groups, the anterior pair being usually larger than the others; they are surrounded with transverse and oblique rings. The tarsi usually end in a pair of stout claws, and there is often a sucker on a long pedicel; on one or more of the legs the sucker may be wanting, and is then replaced by a long hair. The capitulum is prominent, and the three-jointed palpi are pressed closely to the sides. The mandibles are usually short but may be of considerable length; they consist of two segments, the distal one of which is serrated. The male genitalia are very variable in structure, and are situated between the last pair of legs in the middle line; they consist of a pair of chitinous processes, behind and on each side of which there are circular suckers. In the female there is only one opening, the vulvo-anal slit, which is situated behind the second pair of legs; it becomes a large transverse slit in the fecundated female. During copulation the sexes become attached to each other by their posterior ends. Banks gives the following key to the more important genera:—

Banks' Key to the Genera of Sarcoptinae

1.	Anal opening on the dorsum	2
	Anal opening below	3
2.	On small mammals, not bats; third pair of legs in male without apical suckers	**Notoedres.**
	On bats; third legs in male with suckers	**Prosopodectes.**
3.	Pedicel of suckers jointed; mandibles styliform and serrate near tip	**Psoroptes.**
	Pedicel not jointed; mandibles chelate	4
4.	No suckers to legs of females; parasitic on birds	**Cnemidocoptes.**
	Suckers at least on legs I and II; parasitic on mammals	5
5.	Legs very short; in male the hind pairs equal in size; body usually short	**Sarcoptes.**
	Legs more slender; in male the third pair is much larger than the fourth; body more elongate	6
6.	Female with suckers to fourth pair of legs	**Chorioptes.**
	Female without suckers to fourth legs	7
7.	Hind part of male abdomen with two lobes	**Caparinia.**
	Hind part of male abdomen without lobes	**Otodectes.**

Genus Sarcoptes, Latreille

The species belonging to this genus may be recognized by the characters given in the above key; some additional points are as follows:—The males have no suckers on the third pair of legs and are also devoid of copulatory suckers; in the female the first two pairs of legs have suckers while the others are provided with hairs. The capitulum has well-developed cheeks. The genus contains one species, *Sarcoptes scabei*, de Geer, which is parasitic on man; a number of varieties of it are found on different animals.

Sarcoptes scabei, de Geer. Body oval and marked by fine parallel ridges which are interrupted on the dorsum by seven minute conical spines, arranged in four regular rows. There are two longer spines on the border of the epistoma and three shorter and stouter ones arranged in the form of a triangle on each side behind the origin of the second pair of legs; in addition there are two rows of three larger spines in the posterior part of the body. On each side of the anus there are two long bristles projecting backwards.

This species is the well-known sarcopt of scabies; it burrows into the skin, forming a tunnel at the bottom of which the female deposits her eggs; her presence causes irritation which results in time in the formation of an eczematous condition of the skin.

Life history of Sarcoptes scabei

The eggs hatch in about five days and the larva which emerges sheds its skin three times, the last moult resulting in the formation of the nymph. These are of different sizes, and when the next moult takes place the smaller become males and the larger females; the former do not moult again, but the latter pass through another change, when they become mature. The males often remain at the surface of the skin, and die as soon as the act of copulation is completed.

Sarcoptes scabei has many varieties which have been described as species by different observers; they are mainly characterized by differences in size, and this is said to depend on the thickness of the skin of the host. Those parasitic on the Pachydermata are the largest, next in size are those found on the Carnivora, next those on the Ruminants, and so on. There is a variety of *Sarcoptes scabei* for almost every common domestic animal; it should be noted that they are not restricted to one species of animal but may pass from one to the other.

GENUS PSOROPTES, GERVAIS

Body oval; capitulum conical, considerably elongated and without cheeks (cp. *Sarcoptes*). The legs are short and thick, particularly the anterior ones, and, unlike those of *Sarcoptes*, they are visible outside the lateral margins of the body; the suckers are carried on a long three-jointed pedicel. The male has copulatory suckers and is armed with two knob-like prolongations.

This genus also contains one species, *Psoroptes communis*, with a number of varieties related to the species of the host; they can only be distinguished from each other by their size. These sarcopts do not burrow into the skin, but live among the scabs produced by their irritating bites.

GENUS CHORIOPTES, GERVAIS

Body oval; capitulum conical and as broad as it is long, without cheeks. Legs are long and thick and visible beyond the sides of the body. The suckers are broad and carried at the end of a short simple pedicel. The male has copulatory suckers and abdominal projections.

This genus contains two species, *Chorioptes symbiotes*, Verh., which lives in colonies among the scabs it produces by its bites, and *Chorioptes cynotis*, Hering, which lives in the concha of the dog, cat and ferret.

FAMILY ERIOPHYIDAE

This family contains a large number of minute acari of peculiar form which live on plants and cause galls, differing from those made by insects, in that there is an opening through which the acari can pass. The adult has only two pairs of legs, situated at the anterior end of the body; the posterior pairs are wanting, and appear to be represented by long delicate hairs; they have no respiratory organs and are thus placed in the group Zemiostigmata. They cause considerable damage to useful plants.

FAMILY DEMODICIDAE

This family contains the sebacic mites, which belong to the single genus *Demodex*; the species are parasitic in the sebaceous glands and hair follicles of man and animals. They are extremely small, have elongated transparent bodies with eight short mole-like legs. The rostrum is short and trapezoidal in shape; the mandibles and maxillae are styliform, and the palps are closely applied on the lower surface of the rostrum. The abdomen tapers to the posterior end, which is rounded and transversely striated above and below; the legs are short and consist of three joints; respiratory organs are wanting. The egg is fusiform in shape and there are one larval and two nymphal stages, the latter closely resembling the adults.

Demodex folliculorum, Simon, is parasitic in the sebaceous glands of man. The female measures ·38 mm. in length and the male ·30 mm.

Demodex canis, Tulk. This species is regarded as a variety of *folliculorum*, and, as its name implies, is parasitic on the dog; it is, however, smaller, the female measuring ·25mm. in length and the male ·22 mm. It produces little swellings in the skin which become pustular and cause intense itching; these swellings are usually full of the mites and when there are a large number of them the animal emaciates and may eventually die.

Demodex phylloides, Caskor, is an allied species which lives in the skin of swine and causes small white tubercles. The animals do not appear to be affected by it.

Demodex bovis, Stiles, has been recorded from the skin of cattle in the United States; it also causes small tumours which become abscesses and often damage the hide.

COLLECTION AND PRESERVATION

Mites which are parasitic on small rodents, such as rats and squirrels, may be collected and their life histories studied by placing the animal in a wire rat trap and surrounding it with a cloth as described for fleas. The female mite always leaves its host to lay its eggs, and these may be collected from the cloth. By combing the hair of the host numbers of the immature stages may be collected; the mites which live on the blood of birds may be studied in the same way. Many snakes and lizards harbour acari, and these are often found below the scales or attached to the cornea. They should be picked up with a moistened brush, never with forceps, and placed in seventy per cent alcohol. Mites which attack insects should either be preserved along with the insect to which they are attached or scraped off with a fine knife and preserved separately.

The various free-living forms may be collected by drawing a net over leaves and grass, by turning up old heaps of manure, decaying barks of trees, and stones; when attached to a plant the leaf or twig should be cut off and the whole placed in spirit.

Examination and dissection

Mites can be readily examined in the fresh condition by placing them in a small drop of distilled water on a slide, and covering it with a coverslip; as the water evaporates it can be replenished by means of a pipette. In this way it is often possible to identify specimens without having to make a cleared preparation. This is, however, necessary when closely allied species have to be separated. Mites are difficult to dissect, but it is often possible to remove most of the organs by placing the specimen in a drop of saline solution on a slide and nicking the integument with a fine needle. Sections are difficult to obtain and double embedding is imperative.

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CHAPTER X

SECTION I

ARACHNIDAE INCERTAE SEDIS: THE ORDER PENTASTOMIDA: TONGUE WORMS: FAMILY LINGUATULIDAE

Endo-parasitic Arachnida with an elongate, vermiform and annulated body. Mouth parts rudimentary and surrounded by two pairs of hooks which probably represent rudimentary mandibles and maxillae. Respiration is cutaneous. Circulatory system wanting.

Biological position of the Linguatulidae

The Linguatulidae comprise a small group of peculiar vertebrate blood-sucking parasites which in the adult stage closely resemble worms, the body being cylindrical, elongated, and often annulated. In spite of this superficial resemblance they are in no way related to the worms, but are in reality degraded arachnids which, in correlation with their mode of life, have lost nearly every trace of their arthropod ancestry. The larval stage, however, still has two pairs of short legs armed with hooks, and resembles the degenerate *Demodex* and *Pediculoides*; the muscles of the Linguatulidae are striated, another character common to Arachnids.

Relation to disease

The Linguatulidae are chiefly found in the respiratory passages and the alimentary tract of carnivorous animals and snakes; rarely in birds and fishes. A few have been recorded from man, and the probability that they are more widely distributed than is known at present, adds to their importance as human parasites. *Linguatula serrata*, Frölich, has been found both in its larval and adult stage in the lung, liver and spleen of man, and Darling has recently recorded a larva of this species from the lung of a native of Central America. In 1847 *Porocephalus armillatus* was discovered by Pruner in the liver of Negroes in Cairo; subsequently it was found by others in the same situation. *Porocephalus moniliformis* has been found twice in man, once in the small intestine under the peritoneum in a native of Sumatra, and again in the liver of a Filippino. Several other doubtful species have been recorded from man by Welch, Osler, and Flint. It is not clear, however, as to whether the invasion of the human body by tongue worms actually results in a disease condition, somewhat loosely spoken of as Porocephaliasis; the parasites have never been recorded in large numbers and it would appear that the few which have been found represent an accidental infection, and that man is not the true host of any of the species.

In 1907 the senior author, while studying the haemogregarines of snakes, noted the occurrence of encysted gregarine-like parasites in the salivary glands of *Porocephalus pattoni*; these have since been described by Prowazek, who regards them as the developmental stages of the blood parasites of the snakes; there is at present no proof that this is the case.

EXTERNAL ANATOMY

General structure

The adult linguatulid is vermiform in shape and of a white colour; it may be cylindrical throughout, or the ventral surface may be flat and the dorsal rounded. The anterior end—that by which it fixes itself to its host—is broad and rounded, and the posterior extremity is attenuated. The cephalothorax—the rounded anterior portion—merges into the body, which forms the largest part of the animal. The integument may be divided up into annuli or segments, and is pierced by numerous minute pores which are the orifices of dermal glands. Legs are wanting.

Mouth parts

The mouth is situated on the ventral surface of the cephalothorax and is usually subterminal, but may be terminal; it lies in the middle line and is oval in shape, and is surrounded by a well developed chitinous framework (Plate LXXXVIII, fig. 4). Lying on each side of it there is a pair of chitinous hooks which can be retracted into grooves; in the living condition they are retracted and protracted like the claws of a cat, and it is evident that the animal uses them not only for fixing itself to the tissues of its host, but for puncturing the membrane in order to draw blood, for the adult linguatulid is a blood-sucker.

The sexes are distinct, and the male is always smaller than the female; the genital opening of the latter is situated at the posterior end of the body just in front of the anus; in the male it is situated high up near the junction of the cephalothorax with the abdomen.

The most valuable taxonomic characters are the number of annuli, the shape of the cephalothorax and the structure of the hooks.

CLASSIFICATION

The family Linguatulidae is divided into three genera, which may be distinguished by the following key :—

1. Body flattened ventrally, rounded dorsally and tapering posteriorly ; haematocoele forming pockets in the lateral rings . **Linguatula.**
   Body not so flattened 2
2. Body cylindrical and ringed ; haematocoele continuous . . **Porocephalus.**
   Body cylindrical but not ringed . . . . **Reighardia.**

Sambon has created a fourth genus, *Raillietiella*, for three species in which the posterior extremity is bifid, the female sexual opening is at the anterior end of the abdomen, and in which there are three vesicular protuberances around each hook pit.

GENUS LINGUATULA, FROLICH

Linguatula serrata, Frölich. The male is white and measures from 18 mm. to 20 mm. in length and 3 mm. in width ; the female is greyish white and measures from 80 mm. to 100 mm. in length and from 8 mm. to 10 mm. in width in front and 2 mm. behind. This species is widely distributed in Europe, and appears to be common in certain parts of France ; it is parasitic in the nasal and respiratory passages of a number of animals, including the dog, fox, wolf, horse, goat and sheep ; the larva is found in the horse, sheep and the ox ; the dog appears to be the true host.

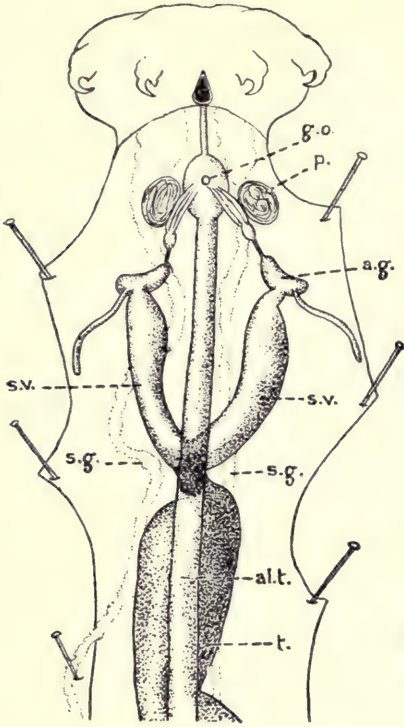
Life history and bionomics

The eggs are expelled from the nasal cavities of the dog by the act of sneezing and fall on the ground, from which they may be blown about ; if they fall on grass on pastures, as may occur in the case of sheep-dogs, they may be ingested by sheep and cattle, in the alimentary tract of which they hatch out. The larva bores its way through the intestinal wall and becomes lodged in some organ, usually the liver, where it passes through a quiescent stage, changing once or twice until the nymph is formed. This stage is very similar to the adult, but has numerous spicules on the skin ; it wanders about in the body of the host until it reaches the respiratory tract, up which it passes to find its way out eventually through the trachea. It is not quite clear as to how it gets back to the dog, but it is probably either through the alimentary tract or up the nose ; it is always found in the nasal cavity, where it becomes sexually mature.

GENUS POROCEPHALUS, HUMBOLT

This genus contains about twenty species, many of which are very imperfectly known ; further study will probably reduce the number

PLATE. LXXXVIII.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p.
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Fig. 1.

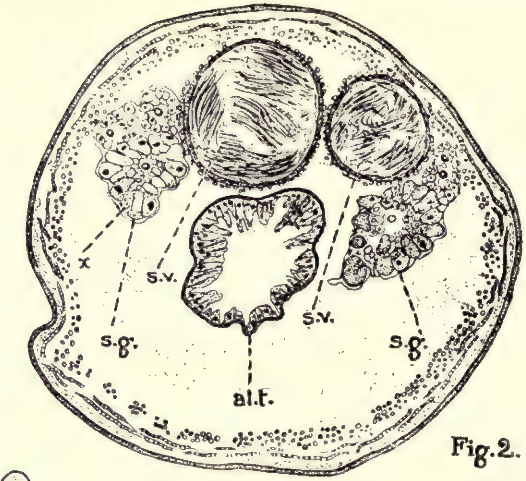
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Fig. 2.

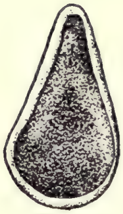
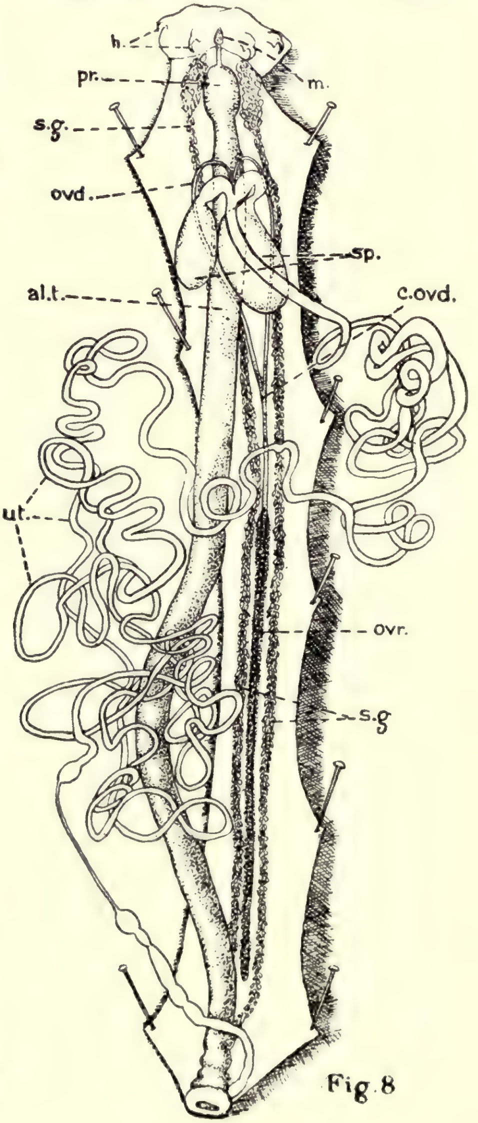


Fig. 4.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ut.
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s.g

Fig. 8

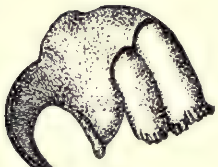

Fig. 5.

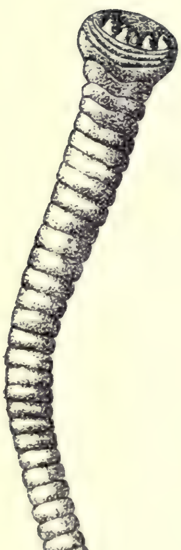

Fig. 3.

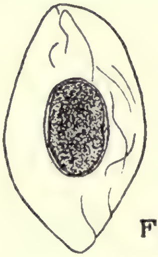

Fig. 6.

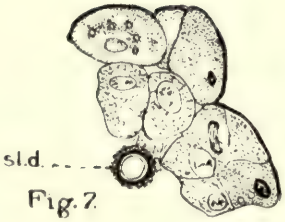

Fig. 7.

PLATE LXXXVIII

Figure 1. Dissection of *Porocephalus pattoni*, ♂, displaying reproductive organs. a.g., accessory gland. al.t., alimentary tract., g.o., genital opening. p., penis. s.g., salivary gland. s.v., seminal vesicle. t., testis. × 10.

Figure 2. Transverse section through *Porocephalus pattoni*, ♂. al.t., alimentary tract. s.g., salivary gland. s.v., seminal vesicle. x., protozoal cyst. × 20.

Figure 3. *Porocephalus pattoni*, ♂. × 3.

Figure 4. Mouth of same.

Figure 5. Isolated hook of same.

Figure 6. Egg of same.

Figure 7. Transverse section through salivary gland of same. sl.d., salivary duct.

Figure 8. Dissection of *Porocephalus pattoni*, ♀, displaying the internal organs. al.t., alimentary tract. c.ovd., common oviduct. h., hooks. m., mouth. ovd., oviduct. ovr., ovary. pr., pharynx. s.g., salivary gland. sp., spermathecae. ut., uterus. × 2.

PLATE LXXXVII

already described. *Porocephalus moniliformis* and *P. armillatus* are the two species which have been carefully studied; both of these have been found in man.

Porocephalus moniliformis, Diesing. Male with twenty-six rings and female with twenty-eight to thirty-two rings; both sexes are somewhat slender and taper towards the posterior extremity.

The adult stage is found in the lung of the Indian Python (*Python molurus*), also in the reticulated python, *P. reticulatus*; the nymph has been recorded from man, monkeys, the tiger, civets, the cat and the dog. Its life history is unknown. It is distributed throughout India, Indo-China, Philippines, Sumatra and Java.

Porocephalus armillatus, Wyman. Body slightly flattened on its anterior surface, and tapering from the middle towards the extremity. Male with about sixteen rings and female with twenty to twenty-two rings; each of the rings is separated from its fellows by a wide space.

The adult of this species has been found in the lungs of the African Pythons, *Python sebae* and *P. regius*, and in a number of other snakes from Africa; the larva has been found in man as already noted, and in monkeys, hedgehog and the lion. The nymphs have also been found in these animals. Its complete life history is not known.

Porocephalus crotali, Humbolt. Body cylindrical, incurved, and slightly flattened on the ventral face; female surrounded by about eighty flat annuli. It is parasitic in the lungs of the rattle snakes of South America; its life history is unknown.

Porocephalus pattoni, Stephens. Body greyish white, cephalothorax globular and distinctly demarcated off from the abdomen; posterior extremity blunt. The number of rings varies from thirty-six to forty; there are usually thirty-eight in the male (Plate LXXXVIII, fig. 3). An isolated hook is depicted in fig. 5 and the mouth ring in fig. 4; the egg is shown in fig. 6. This species is parasitic in the lung of the rat snake, *Zamenis mucosus*. Its life history is unknown.

INTERNAL ANATOMY

PLATE LXXXVIII

Alimentary canal

The *alimentary tract* of a linguatulid is comparatively simple. The mouth is oval in shape and is situated on the ventral side of the cephalothorax, between the inner pair of hooks, and is surrounded by a strong chitinous framework. It opens into the pharynx, which is a short tube leading upwards and backwards to open into the oesophagus; the pharynx or sucking pump is actuated by certain muscles attached to its walls. At the junction of the oesophagus with the intestine there is a marked dilation which probably represents a proventriculus. The intestinal canal is a broad cylindrical tube which lies in the middle of the body and ends in a transverse slit, the anus, just above the caudal end on the ventral side; in the living condition it is of a dark brown colour, due to the digested blood it contains, and exhibits slow peristaltic movements. On section it is seen to be a wide tube lined by a row of large cylindrical cells, with deeply staining nuclei, attached to a delicate basement membrane; around this there is a layer of circular muscular fibres, and external to these there are a few longitudinal muscular bands.

Salivary glands

Closely applied to the sides of the alimentary tract are the *salivary glands*, which consist of groups of acini surrounding a large duct. (Plate LXXXVIII, fig. 2. s.g). The cells are composed of two kinds, large finely granular cells with small deeply staining nuclei and smaller vacuolated cells with somewhat larger nuclei. These cells are arranged in groups to form lobules, from which delicate ducts carry the secretion to the main channel. In the salivary glands of *Porocephalus pattoni* it is quite common to find the encysted stage of a protozoon (fig. 2, x), which is believed to be the sexual stage of the haemogregarine of the snake, lying in between the salivary cells; all stages in the development may be seen, from small cysts to large ones full of daughter cysts containing sporozoits.

Female reproductive organs

On opening a female linguatulid the reproductive organs come prominently into view (fig. 8). They consist of a median ovary, a pair of oviducts, a pair of spermathecae and an extremely long uterus, which is coiled up and when full of eggs occupies almost the entire body cavity. The *ovary* lies between the salivary glands and is closely applied to the dorsal surface of the intestinal tract in its lower half; it is of a dull white colour and exhibits a finely lobulated appearance, due to the presence of young ova. Its structure resembles very closely that of the corresponding organ in the ticks. About the junction of the middle and upper third of the body it divides into two delicate *oviducts*, which after a short course in contact with the intestinal tract dip down on each side to the ventral surface, and pass round the intestine to unite to form a short common duct, into which enters the duct formed by the junction of the two spermathecae. These organs are situated on the ventral surface on each side of the intestinal canal; they may be recognized by their white colour and saccular shape. The *uterus* arises from the junction of the ducts of the spermathecae; it is a long coiled tube, which in the mature female is loaded with an immense number of ova and when stretched out may measure (in *Pr. pattoni*) as much as six inches. It opens at the posterior end just in front of the anus. The ova contain a central granular mass, and are surrounded by a chitinous covering which is obviously designed to prevent desiccation.

Male reproductive organs

The male reproductive organs consist of a median testis—in some forms (*Linguatula*) it is a paired organ—a pair of spermatic ducts, an accessory gland on each side and a paired penis of complicated nature. The *testis*, which is situated in the same position as the ovary in the female, is a large white saccular organ; it divides into two ducts (seminal vesicles, fig. 1, s. v.) which surround the intestinal canal and pass to the ventral surface, where they end in a tubular dilatation which has attached to it a long finger-like ejaculatory duct. From the upper end of the dilatation the tube leads to a chitinous sac which has attached to it a coiled penis. The organs unite and open at the genital pore, which is situated on the ventral surface just below the cephalothorax. The method of copulation has not been observed.

DISSECTION

All the organs of a linguatulid can be readily displayed by the following method. Pin the specimen down in the dissecting trough, ventral side upwards, with two fine pins; one pin should be passed through the cephalothorax well in front of the mouth and the other behind the anus, so that none of the internal organs will be injured. With a fine pair of forceps a bit of the integument is picked up and snipped through with scissors; one end of the cut is now elevated and one blade of the scissors passed between the skin and the internal organs, and the integument is slit up along the middle line. It should be pinned out at intervals as shown in Plate LXXXVIII, fig. 1., and the organs unravelled, care being taken not to damage either the uterus or the intestine. Very beautiful sections may be obtained by cutting the animal into small pieces and embedding them in paraffin, keeping them as short a time as possible in the various fluids.

COLLECTION AND PRESERVATION

In tropical countries snakes of different kinds harbour species of *Porocephalus*, and they are nearly always to be found in the lung.

Almost every rat snake examined in Madras harbours one or more specimens of *Porocephalus pattoni*; they are often deeply embedded in the lung tissue, the whole of the cephalothorax being concealed. They should not be removed by traction or the body may break. The lung of the snake should be dissected out and the whole placed in a Petri dish full of saline solution. The linguatulids often free themselves, but if this does not happen there is usually a tight constriction of fibrous tissue behind the cephalothorax, which must be cut through with scissors before the specimen can be freed. They will live for several days in saline if the precaution is taken to renew it; the females under these conditions pass out enormous numbers of ova, which settle at the bottom of the dish and form a granular debris.

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CHAPTER X

SECTION 2

CLASS CRUSTACEA: SUBCLASS COPEPODA: ORDER EUCOPEPODA: GENUS CYCLOPS: WATER FLEAS

THE class Crustacea, which includes such familiar animals as the crabs, lobsters, shrimps and wood-lice, contains also a host of small aquatic arthropods, among which are the water fleas (*Cyclops*), so named on account of their short, jerky movements when swimming. The subclass Copepoda in which the genus *Cyclops* is placed contains a great variety of crustaceans with very diverse life histories; some are ectoparasites of marine animals, as for instance the common *Argulus*, or Carp louse, a flat, leaf-shaped form provided with suckers by which it fixes itself to fish; others are endoparasites and live in such situations as the mouth and under the skin of fish. Many of these parasitic forms illustrate the degeneration of structure which so often accompanies the assumption of the parasitic habit.

The great majority of copepods are free-living and are for the most part of small size; they are abundant in both fresh and salt water in all parts of the globe; the species belonging to the genus *Cyclops* are the only copepods which are of known importance. For a general account of the class the reader is referred to the article in Lankester's *Treatise on Zoology*, Part 7, fasc. III.

GENUS CYCLOPS

Minute Eucopepoda *in which the first thoracic segment is united to the six head segments to form a cephalothorax, which is covered by a carapace produced into a rostrum in front, and which bears on its dorsal surface a median eye; the cephalothorax is armed with diverse appendages. There are in addition five free segments, each provided with a biramose swimming leg; the sixth thoracic segment bears the sexual opening and in the female is united with the first abdominal segment. There are four abdominal segments, the fourth of which has on its dorsal surface the anus, and at its termination a pair of stylets, the caudal fork, produced into feathery plumes.*

Cyclops abounds in the tropics in all large and small collections of fresh water; many of the species are of special importance as they are the invertebrate hosts of the Guinea-worm, *Dracunculus medinensis*. Fedschenko, working in Turkestan, was the first to demonstrate that the embryos of the Guinea-worm undergo some developmental change in the body of *Cyclops*, his observations being confirmed later by Manson in England. Fedschenko believed that when the dracunculus-infected *Cyclops* was ingested by man in drinking water, the worm was liberated by the dissolution of the crustacean, and that it then burrowed into the tissues of its new host, man, and slowly became transformed into the well-known adult worm, which appeared at the surface of the skin on the legs and feet; this observer, however, failed to infect man by means of infected *Cyclops*, and the hypothesis remained *sub judice*. Leiper next attacked the problem, and he was able to show that, when an infected *Cyclops* was placed in a two per cent solution of hydrochloric acid, the crustacean was killed, but the contained larva of *Dracunculus* was stimulated into great activity and soon escaped from the body of its host. The obvious conclusion was that the hydrochloric acid in the stomach of man or an animal would have the same effect. In order to test the hypothesis Leiper fed a monkey with a large number of *Cyclops* which had been infected six weeks previously, and which were known to contain mature larvae of the Guinea-worm; six months later, when the monkey died, he found in the connective tissue five worms, which resembled the adult *Dracunculus*. This experiment has yet to be confirmed.

Relation to Disease

According to Fedschenko the Guinea-worm embryo penetrates the *Cyclops* by piercing it between the segments on the ventral surface, and Wenyon states that he has seen this phenomenon take place in his experiments in the Soudan. Leiper, on the other hand, is of the opinion that the embryos enter by way of the alimentary tract. Roubaud, in a recent paper, records having experimentally confirmed Leiper's observations, and maintains that the infection is intestinal. He placed a large number of *Cyclops* in water which had been previously rendered cloudy with embryos of *D. medinensis*, and found that six hours later many of the *Cyclops* contained groups of embryos in the region of the mid-gut; the embryos were very active and did not appear to be affected by the digestive juices of their host. In the fresh condition none of the embryos were seen in the body cavity, but in sections of the host some were seen lying in the body cavity close to the mid-intestine. Twenty-

Development of D. medinensis in Cyclops

PLATE. LXXXIX.

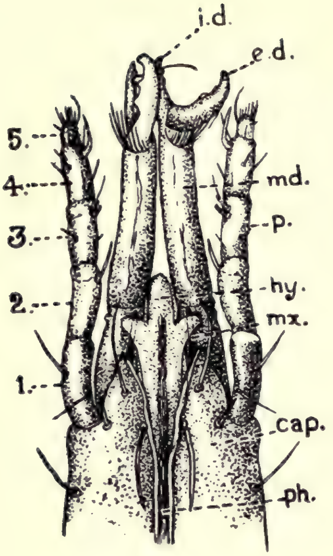
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Fig. 1.

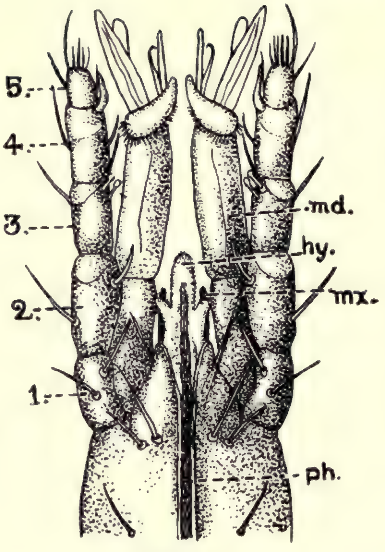
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Fig. 2.

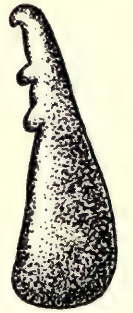
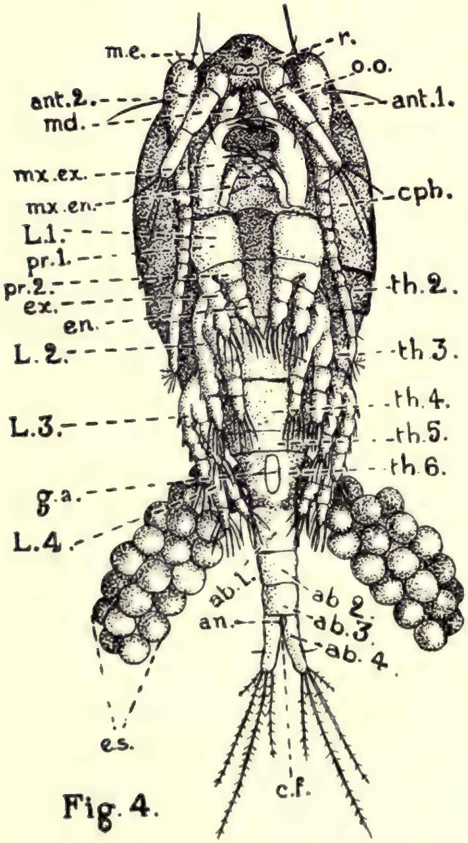


Fig. 3.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th.6.
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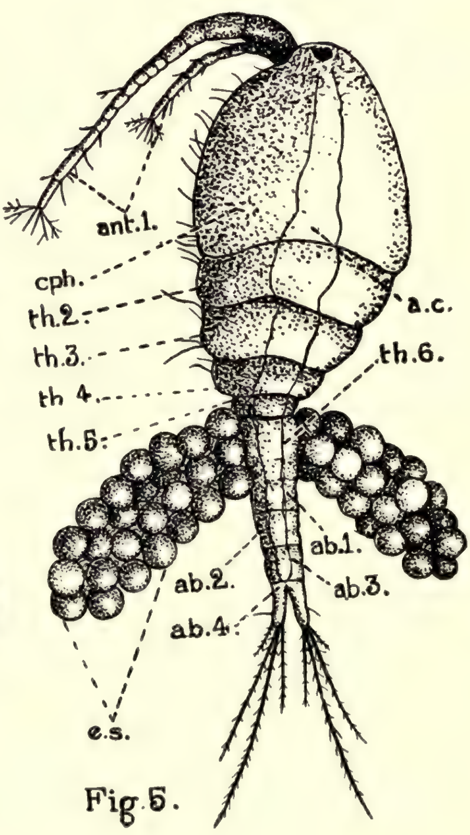
Fig. 4.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ab.4.
e.s.

Fig. 5.

PLATE LXXXIX

Figure 1. Capitulum and mouth parts of *Laelaps sp.*, ♀.
Figure 2. Capitulum and mouth parts of *Laelaps sp.*, ♂. cap., capitulum. e.d., external digit. hy., hypostome. i.d., internal digit. md., mandible. mx., maxilla. ph., pharynx. 1, 2, 3, 4 and 5., First, second, third, fourth and fifth palpal segments.
Figure 3. Digit of same, highly magnified.
Figure 4. Ventral view of *Cyclops sp.*, ♀, highly magnified.
Figure 5. Lateral view of same.

Reference Letters to figures 4 and 5

ab. 1.	First abdominal segment.	L-2.	Leg. 2.
ab. 2.	Second ,,	L-3.	Leg. 3.
ab. 3.	Third ,,	L-4.	Leg. 4.
ab. 4.	Fourth ,,	m.e.	Median eye.
a. c.	Alimentary canal.	md.	Mandible.
an.	Anus.	mx.en.	Maxillary endopodite.
ant. 1.	Antennule.	mx.ex.	Maxillary exopodite.
ant. 2.	Antenna.	o.o.	Oral opening.
c.f.	Caudal fork.	pr. 1.	First protopodite.
c.ph.	Cephalothorax.	pr. 2.	Second protopodite.
en.	Endopodite.	th. 2.	Second thoracic segment.
e.s.	Egg sac.	th. 3.	Third thoracic segment.
ex.	Exopodite.	th. 4.	Fourth thoracic segment.
g. a.	Genital aperture.	th. 5.	Fifth thoracic segment.
L-1.	Leg. 1.	th. 6.	Sixth thoracic segment.

four to forty-eight hours after the *Cyclops* were placed in contact with the embryos all had left the mid-gut and were found lying in the body cavity; no trace of digested embryos was seen in the alimentary tract. Roubaud states that the naupilus larva of *Cyclops* is just as susceptible to infection as the adult crustacean, and that it is not uncommon to find three or four embryos in a single *Cyclops* larva.

Roubaud has studied the development of the embryo in *Cyclops* in Dahomey, and has confirmed the observations of Leiper. The embryo may remain unchanged for ten days after entering the invertebrate host, but as a rule the first sheath forms about the eighth day (larval stage), and by the fourteenth day it enters on its second stage. The pointed tail of the young embryo is replaced by a short blunt process, and though the striation on the integument is still visible, it is much less apparent. The larva is cylindrical in shape and measures 0·5 mm. in length, and is much less motile than in the first stage. Forty-two days later it has increased in size and now measures 0·6 mm.; its mouth develops into two distinct lips, and the posterior third of the body becomes of a yellowish brown colour. At this stage the larva is entirely quiescent and lies coiled up in the body cavity of its host. Roubaud states that no papillae could be made out at the end of its body, and that the tail is conical and not trilobed. Although he carried out several transmission experiments by feeding monkeys with infected *Cyclops* he was unable to infect them with Guinea-worm. Roubaud believes that endemic dracontiasis depends on a complex equilibrium between, (1) the time required for the annual development of the adult female *D. medinensis* in man, (2) the regular recurrence of the necessary seasonal conditions, and (3) the conditions of human existence which favour transmission by *Cyclops*.

Anatomy of Cyclops (Plate LXXXIX, figs. 4 and 5)

The cephalothorax and its appendages

The body of *Cyclops* is pear-shaped, the broad end being anterior and the dorsal surface convex (Plate LXXXIX, figs. 4 and 5); the posterior end is attenuated and ends in two blunt processes armed with feathery stylets. The cephalothorax is completely covered by a convex plate of chitin, the *carapace*, which is produced around the sides towards the ventral surface. Arising from each antero-lateral border on the ventral surface is a long attenuated process known as the *antennule*; this consists of fourteen segments, of which the basal and apical are the longest, the intermediate segments being very short; the apical segment is armed with a number of branched spines. The antennules can be raised away from the body or pressed close into the ventral surface; they are the principal organs of locomotion, the animal propelling itself in short jerks by rapidly flexing them. The *antennae* are inserted just internal to the insertion of the antennules and are uniramous; each antenna consists of three segments, the basal one being the shortest, the apical segment armed with a few long spines. Between the insertions of the antennae is a short spinous process, the *rostrum*, and directly above this on the dorsal surface is a large pigmented spot, the median eye.

The mouth parts

Further back on the ventral surface and in the median line is the mouth opening, on each side of which are the mandibles and maxillae; the *mandible* consists of a short bar of chitin with the inner end produced into a point, and is furnished with numerous short stiff spines. The *maxillae* are a little further back and are much more conspicuous; each maxilla consists of two segments, of which the external one, or *exopodite*, is the larger, and is shaped like a claw, its tip being bidentate; the *endopodite* is much smaller, extending up to about half the length of the exopodite; it is armed with stiff spines.

Thoracic and abdominal segments and their appendages

The first pair of legs arise from the sides of the first thoracic segment, which in this copepod has become fused with the head. The second pair appear to arise from the first thoracic segment, in reality from the second segment. Each leg is biramose and consists of a large basal segment, the first *protopodite*, and a shorter apical segment, the second protopodite, to which are attached the endopodite and exopodite, each consisting of three segments, the apical one of which is armed with long stout spines. The second, third, and fourth legs arise from the corresponding thoracic segments; the fifth, like the preceding ones, is free and is armed with a pair of vestigial limbs. The sixth segment bears the genital aperture, and in the female is united to the first abdominal segment; the egg sacs are attached at its sides. The fourth abdominal segment is bifid, and ends in two blunt processes armed with long feathery spines; the anal opening is situated on the dorsal surface in the middle line. The abdominal segments are without any appendages.

The alimentary tract is simple, extending directly from the mouth to the anus, with a dilated portion, referred to as the stomach, in the middle. It is in the stomach that the embryos of *Dracunculus medinensis* are found.

The life history of *Cyclops* is easily followed under artificial conditions. An egg-bearing female is selected, and placed in a vessel of water which

Life History

has been freed from all visible animal life; a small piece of green vegetable matter, such as a blade of grass or the leaf of a water plant, is placed in the vessel to provide food, after having been carefully washed. In a few days, sooner or later according to the temperature, the eggs hatch out, and the larvae can be seen as minute white specks floating about in the water. The young larva is termed a 'naupilus'. It consists of an oval body with three pairs of appendages, the posterior two of which are biramose, and probably represent the mandibles and maxillae, the anterior pair representing the antennules. They are all used as organs of locomotion. The alimentary tract is easily visible through the transparent integument, and may be seen pulsating in the fresh condition. The larva moults at least twice, and after each change several buds appear, which later on become the legs.

Bionomics of Cyclops

Graham, in his work on the Cyclopodae of the African Gold Coast, points out that in any one neighbourhood there are a large number of different species of *Cyclops*, the habits of which vary; some are surface feeders, while others only live at the bottom. Many of the species are found only in foul water, while others can only live in fresh water. Quite a number of the species have the habit of climbing up stalks of water-weeds, surrounded by a drop of water which they carry with them; some never leave the water. Lastly, there are some species which only occur in streams, and are never found in ponds or wells. On the Gold Coast Graham noted that certain species appear at particular times of the year and that there is quite a marked difference in the seasonal prevalence. It should also be remembered that a number of species of *Cyclops* have their natural nematode parasites which have nothing to do with the Guinea-worm.

In conducting any experiments with Guinea-worm and *Cyclops* negative results may be entirely due to a choice of an unsuitable species, and it is therefore very important to study the different species, their geographical distribution, seasonal prevalence and habits.

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CHAPTER XI

LABORATORY TECHNIQUE

THE examination of insect tissues is conducted for the most part by ordinary laboratory processes, descriptions of which are to be found in the numerous excellent textbooks on the subject. The tissues present, however, certain peculiarities, and though the principles underlying the methods are the same, some modifications are necessary. The chief difficulties met with are due to the minute size of the objects, the great difference in density between the exo-skeleton and the internal organs, and the intimate manner in which the air-containing tracheae are connected with the tissues. The following account deals only with methods which the authors have used themselves, and does not pretend to be an exhaustive one.

The Dissecting microscope

A word is necessary with regard to the dissecting microscope, which is an important part of the laboratory equipment. For ordinary work a simple type, such as can be purchased, complete with hand rests, mirror, and lenses magnifying ten and twenty diameters, for two pounds or so, is sufficient; a satisfactory though not very convenient one can be improvised by fitting a pocket lens on an upright stand, and placing underneath it a large slide, one-half of which is blackened with ink, or covered on one side with black paper. For more elaborate dissections a good binocular microscope, with objectives and eye pieces capable of giving a magnification of at least forty diameters, is essential. Such an instrument finds many uses apart from dissection, its large field and stereoscopic vision rendering it particularly helpful in the performance of many delicate manipulations. If it is fitted with an illuminating apparatus, as can be done at a slight extra cost, it affords quite the most convenient means of examining macroscopic specimens, such as flies, larvae and pupae. Specimens which are not pinned are best mounted for examination by fixing them, at the desired angle, to a piece of plasticine, which is placed on a slide.

For the examination of the chitinous structures, cleared preparations, in which the soft parts have been dissolved out, should be made. This

Cleared preparations

is done by macerating the tissue in a solution of potash or soda, which dissolves out the cellular tissues without affecting the chitinous parts. The specimen is then dehydrated in alcohol and mounted in balsam.

The strength of the solution of caustic potash or soda to be used depends upon the thickness of the exo-skeleton and on the temperature at which it is to be applied. For ordinary use a two per cent solution of the former is the most satisfactory, when the specimen is to be left in it at room temperature. An ordinary object, such, for instance, as the proboscis of the house fly when dissected from the head, will become sufficiently cleared and transparent after two or three days in such a solution. For more chitinous and more opaque objects, one can either increase the strength of the solution or use a higher temperature, such as that of the paraffin oven, which forms a convenient receptacle for the specimen, or simply allow the solution to act for a longer period. For rapid work specimens can be boiled in a ten per cent solution, but this has the disadvantage of sometimes distorting the preparation through the sudden expansion of the contained air; there is also a considerable risk of losing a small object if it is boiled in a test tube.

There are two points to be noted in the manipulation. In whole insects the communications between the exterior and the soft tissues are very restricted, and it is advisable to make sure that the solution will have free access to the interior by making a small cut in some unimportant part of the integument, or by pulling off the legs and wings if these are not required. Secondly, chitinous structures appear darker when in a watery solution than when in balsam, and the clearing should accordingly be stopped at a point when the specimen appears darker than is really required.

Soft tissues which have been fixed in alcohol take much longer to dissolve than when fresh, and if the specimen is not well opened up much of the pigment of the chitin will be dissolved before the internal organs are got rid of. Fresh or dried specimens should accordingly be used for making cleared preparations.

To make a cleared preparation of any part, or of the whole of a small arthropod, proceed as follows. Place the specimen in potash solution, of a strength and at a temperature which are determined by the circumstances, till cleared. Then wash in tap water to get rid of the alkali. A few minutes is sufficient for this; then place in fifty per cent alcohol for at least twenty minutes—more does no harm—then in ninety per cent, and finally in absolute alcohol. Then transfer to clove oil, and after a few minutes mount in balsam. The times for which the specimen is to be left in the various solutions depend upon its size and also upon the amount to which it has been opened up to allow of free penetration of the fluids. Prolonged application does no harm in ordinary work, and the specimen may be left overnight in any stage if convenient.

When studying the finer details of the chitinous parts it is best to complete the dissection when the preparation has been cleared and taken up to clove oil, as the object can then be dissected on the slide on which it is to be mounted, thus obviating the risk of losing during the manipulation any parts which are too small to be seen without the aid of a microscope. It must be borne in mind, however, that prolonged immersion in either alcohol or xylol, and to a lesser extent clove oil, makes chitin brittle; cleared preparations which require further dissection before mounting should, therefore, be carried through as rapidly as possible.

Bleaching of chitinous parts

Very thick chitinous parts may be rendered more easy to examine by bleaching them after clearing. This is easily accomplished by the action of chlorine gas, generated in a test tube from dilute hydrochloric acid and chlorate of potash, or from chloride of lime. It is best to allow the gas to generate for a few minutes, until the liquid is a rich yellow colour, and then to put it aside till gas is no longer given off. A few minutes in this solution will render the densest parts transparent. If the specimen is placed in the mixture while effervescence is going on there is always a risk of losing it, if it is small.

Staining cleared preparations

Delicate chitinous objects, such as the wings of small flies, or the thin plates in the wall of the thorax, may be stained after a short period of clearing. It is, of course, necessary to wash the specimen thoroughly to get rid of the alkali before applying the stain. Either a strong solution of watery eosin, which stains the membrane between the chitinous parts more than the chitin itself, or carbol fuschin, may be used. The length of time of staining depends upon the density of the specimen, and it is convenient to overstain in all cases, as either of these stains is easily washed out by a trace of acid.

When dealing with any minute object in an opaque solution great care should be taken that the solution is filtered before use, and that there are no particles of dust in the vessels used. A little care in this respect will obviate the risk of mistaking a particle of dust or deposited stain for the specimen. To find the specimen after staining, pour out the contents of the tube into a flat white dish, and dilute with water until the solution becomes transparent; when the specimen can be seen remove it to clean water with a pipette or a brush. With carbol fuschin it is often necessary to dilute the fluid to a considerable extent before the object can be picked out, and it is therefore well to use as small a quantity of the stain as possible.

Mounting

Many parts, such as whole heads of small flies, can be mounted in hollow slides. When doing so care should be taken to place an excess of canada balsam on the slide before lowering the cover slip on to the specimen, or a bubble of air may get into the hollow, from which it is difficult to dislodge it. Instead of using hollow slides, compression of the specimen may be avoided by placing a fragment of a thin glass slide, a piece of cover slip, or a thin capillary tube, beside it before lowering the cover slip.

In making cleared preparations when material is abundant, a large number of specimens should be placed in the solution at the same time, and withdrawn at intervals, so that a series is obtained in which the decolorization has progressed to varying degrees; these often present strikingly different appearances.

Dissection of fresh material

The dissection of fresh material is by far the most important method of studying the anatomy, and gives more reliable information than can be obtained by sectioning the parts. When dealing with a parasitized arthropod, it is of the first importance to evolve a sure and rapid method of dissection, and when a large number of dissections of the same organ have to be carried out, the method should be reduced to a routine, carried out without deviation in every case.

Dissecting needles

Dissecting needles as obtained from the instrument makers have too coarse points for fine work, and they have to be ground down on a stone. Two kinds of blades are required, simple points and lancet-like blades. If an emery wheel is available these are easily made, but quite satisfactory instruments can be made with an ordinary grind-stone and a soft razor stone. In making the lancet-blades it is convenient to mark the flat side of the needle point by a notch on the corresponding side of the handle. Only one edge should be ground to a blade, or the needle will bend too easily. The needles must always be finished off carefully on the soft stone, or a piece of pumice soap, to get a smooth surface, otherwise the tissues will adhere to them. The final polishing and sharpening should be controlled by examination under the microscope.

Saline Solution

The saline solution in which insects are dissected should be kept carefully, as it forms an admirable medium for the growth of moulds and other organisms, the presence of which may lead to confusion when examining the tissues for parasites. It is convenient to have it put up in small quantities in test tubes, each tube sufficing for one lot of dissections, any left over being discarded. When working away from a laboratory it may be carried in small capsules such as are used for bacterial vaccines*; when stored in this manner it will, of course, remain sterile for any length of time, and the capsules are not easily broken.

The salt solution usually employed is ·05 per cent sodium chloride. For ordinary purposes there is no special disadvantage in using the ordinary ·075 per cent solution.

Dissection of fresh specimens

As regards the actual dissection, the method to be employed differs so much according to circumstances that no general description can be given. First and foremost, one should always determine beforehand exactly what one intends to get out of any given specimen, and cut away ruthlessly at everything else. Unless material is very scanty, it is a waste of time to endeavour to dissect out the whole of the internal structures from one specimen. The more rapidly a dissection is completed the better, especially in dealing with parasites, for it must be remembered that even the salt solution is an unnatural environment for living cells, and it is possible that parasites may change their form in it, though moderately prolonged immersion does not appear to affect the staining properties of the tissue cells.

The working out of a satisfactory method of dissection in any given case depends upon a knowledge of the anatomy, and particularly of the relations of the internal parts to the exo-skeleton. The alimentary canal, for instance, is attached to the exo-skeleton only at the mouth and at the anus, and is elsewhere only connected with it by the tracheae; the reproductive organs are connected with the integument only at the external opening; the salivary glands lie in the thorax, and may extend to the abdomen, the common duct from the two glands passing through the neck. By freeing the portion of the integument to which the system is attached it is possible to draw it out of the body cavity, severing the tracheae as they appear. All the organs will stand a certain amount of pulling, and as a rule the tracheae will break before the softer tissues.

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* Details of the method of preparing and filling such capsules will be found in Sir A. E. Wright's book, *The Technique of the Teat and Capillary Tube.*

After a few preliminary dissections to get an idea of the general relations of the parts, the exo-skeleton, and any internal processes which may arise from it should be studied, in order to ascertain the route by which the required part can be most easily got out. Usually the larger part of the alimentary canal can be drawn out backwards, by separating the last segment from the penultimate one. The ovaries, if they do not contain large ova, will usually come out by the same route. But neither a distended gut nor a mature ovary will come out unharmed in this way, and one has to make more space by cutting up one side of the abdominal wall. Salivary glands will come out of the thorax if the head is pulled off in many cases, but cannot be expected to do so if they pass down to the abdomen and have a large tracheal supply. The proventriculus of *Tabanus* will not come out of the thorax backwards on account of the small aperture left by the mesophragma. In ticks the only way to get at any of the organs is to open up the dorsal wall. In every case the method of dissection has to be decided on from a consideration of the anatomy of the parts. Where the gut is a distensible organ, as in the case of *Tabanus*, if it should be necessary to dissect it out when full there is nothing for it but to dissect off the integument all round it, for otherwise it is certain to rupture. If mature ova are required, all that is necessary in most cases is to make a slit in the side of the abdominal wall, and to press gently with a needle. One or two of the ova will then slip out. In any case, if the ova are evidently mature, it is advisable to let some of them out in this way before attempting to pull out the gut.

The actual operation of dissection is so much a matter of practice that one cannot do more than offer a few suggestions. In the first place always use a black background for the dissection of internal organs, and have as good a light as possible coming from above. If any muscle gets torn, as it always does in the dissection of the thorax, or if an organ is ruptured, flood the preparation with saline, to wash away the milky fluid. Suck up the saline again with a fine pipette, and add some fresh solution Always remove from the slide all structures not further required, to prevent confusion. Tracheae are recognized at once by their silvery appearance, and should be cut across with the needle, as they hold the other parts in position. Use either as small a quantity of saline as will keep the tissues moist, or else as much as the slide will hold; with any intermediate quantity the surface tension is a source of trouble, as it causes the organs to follow the movements of the needle in a most annoying manner.

Perry has suggested an ingenious method of getting rid of the surface tension. It is due to the presence, even on the most carefully cleaned slide, of a fine film of grease which is probably incorporated in the substance of the glass, since the ordinary solvents for fat will not remove it. Now bile is miscible with both water and fat, and if the slides are smeared with a trace of it before the dissection is commenced, the organs will stay in any position in which they are placed, and do not follow the movements of the needles at all. A few drams of bile from the bladder of a sheep are all that is required for a large number of dissections, as the merest trace suffices for a slide, the surplus being wiped off with a handkerchief.

Use of Bile in dissections

For the dissection of large flies, and especially for ticks, the paraffin trough suggested by Christophers is invaluable. It is made as follows. A glass dish of considerable depth and of a convenient size, say two inches by three, is taken, and filled to a depth of half to one inch with a mixture of paraffin wax and lamp-black, poured in while hot and allowed to set hard. The specimen is pinned down in this by means of entomological pins, and the whole flooded with saline. As the dissection proceeds the various parts can be drawn out of the way and secured with pins ; tracheae, Malphigian tubes, etc., can be fixed by merely pressing them into the wax. The dissection is readily cleaned by agitating the saline with a pipette.

The method of dissection by pulling the organs out of the exo-skeleton is perfectly satisfactory in the majority of cases when looking for parasites, or merely examining a particular piece of tissue, but it is not to be relied on when studying the minute anatomy of the parts, on account of the stretching of the organs which must necessarily take place. In the case of the mosquito the shape of the gut is entirely altered when it is pulled out in the ordinary way. To get a true picture of the organs in their natural relations it is necessary to free them by dissecting off the external wall piecemeal, without pulling on the body contents at all, and then to cut, not pull, the organs which conceal the part to be studied. This is a very laborious and difficult process, and need only be adopted when some special end is in view.

Permanent stained preparations of the internal organs mounted whole are very useful both for demonstration and for the study of the minute structure of the parts, and are in many ways superior to the fresh unstained material. They are especially useful for making drawings of the parts, as one can

Permanent preparations of dissections

deal with them at leisure and can also use the camera lucida more effectively. The following method is a modification of that taught to one of the authors by Dr. Ashworth.

The part to be mounted is dissected in saline in the ordinary way, special care being taken to free it from fat body and other debris, and is severed from the rest of the material. It has now to be transferred to a coverslip, and arranged in such a manner as to best display the anatomy. If the part is large, it may be lifted up on the point of a *clean* needle, and placed in a drop of saline on the coverslip. If a dirty needle, or one with a rough edge, is used, the soft tissue will stick to it, and it may be impossible to detach it. A better plan is to flood the whole slide with saline, remove everything except the part required, and place a coverslip beside it. With an excess of saline it is easy to move the preparation to the coverslip. Then drain off the saline with a pipette and filter paper, and arrange the parts as required; the coverslip will adhere to the slide sufficiently well to allow of the necessary manipulation on account of the moisture between the two.

Fixation

The next step is the one on which the success of the whole process depends. It is necessary to fix the specimen to the coverslip in such a way that no part of it will become detached during the subsequent manipulations, and, as this must be done with a rapidly acting fixative, there is always the risk that the surface tension between the saline solution and the fixative will be enough to either float off the specimen or to disturb the desired arrangement. The important point is to get rid of as much of the saline solution as possible without allowing the tissues to become dry. First remove the excess of moisture with fine points of filter paper, while holding the slide under a low magnification. When this has been done the coverslip should be removed from the slide by pushing it towards the edge, and held between the finger and thumb. When the preparation is just on the point of becoming dry, allow a *small* drop of the fixative to flow from the edge of the slide towards the specimen. The part which it meets will possibly move a little, but in a second or two it will adhere to the glass, and as the alcoholic solution drives the watery saline in front of it, the whole preparation will become opaque and at the same time adherent to the glass. As soon as this has occurred cautiously flood the whole of the coverslip and at once immerse it, face downwards, in a watch glass of the fixative. With simple objects, such as the mid-gut only, or with salivary glands, the fixation is of course quite easy to carry out, but with dissections of the whole gut, with the

Malpighian tubes attached, a good deal of care is necessary in order to preserve the desired arrangement of the parts.

The preparation, when fixed to the coverslip, is treated as a film, and is carried through graded alcohols to absolute alcohol, allowed to remain in this for an hour or so, and then brought back to dilute alcohol of approximately the same strength as the stain; after staining and decolorization it is dehydrated and mounted in balsam on a slide in the ordinary way. The whole operation can be performed without removing the preparation from the original watch glass, the solutions being added and withdrawn with a pipette; square coverslips are more convenient to work with than round ones, as it is easier to withdraw the solution without touching the coverslip.

The preparation may be fixed to a slide in the first instance, instead of to a coverslip, and this is convenient when a series of staining jars with graded alcohols, etc., are available; but it should not be fixed to the slide on which the dissection has been performed, as there is always a certain amount of debris, ruptured fat cells, etc., on this, which take on the stain later and obscure the specimen. Coverslips are on the whole the most convenient and economical.

This method is obviously capable of many modifications to suit particular purposes and circumstances. The following is the routine carried out by the authors for ordinary work.

Taking up the process at the point at which the saline has been removed as far as possible from the coverslip, a drop of Bless'* fluid is placed on one side of the specimen, but not touching it, and the evaporation of the saline watched under the dissecting microscope. When there is only a thin film surrounding the tissue, the fixative is drawn towards the specimen by means of a clean needle, and carried round the several parts, such as the Malpighian tubes, the apical filaments of the ovaries, etc., until they are all fixed to the glass. With a little practice this can be done without any disturbance of the position of the parts. More of the fixative is then added as the tissues become opaque, and finally the coverslip is removed from the slide and inverted in a solid watch glass of the fixative. A label is then attached (a slip of paper fastened to the edge of the watch glass with a touch of Canada balsam), and the watch glass covered up and sealed with vaseline. In half to one hour

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* The junior author is indebted to Dr. Ashworth for the following formula:—

Formalin	7 parts.
Alcohol, seventy per cent	90 ,,
Glacial acetic acid	3 ,,

It should not be used more than ten days old.

the Bless' fluid is replaced by seventy per cent alcohol, and subsequently by eighty per cent, ninety per cent, and absolute alcohol, allowing ten minutes in each of the two first, and one hour in the last; it is then taken back to forty-five per cent alcohol, allowing a few minutes in each strength. The dilute alcohol is then replaced by haematoxylin stain, which is allowed to act for several hours. All dissections should be overstained, and decolorized with dilute acid—one-quarter per cent acetic or hydrochloric—under the microscope. The length of staining and decolorization depend, of course, on the stain and the density of the tissue. Several hours are almost always necessary. When decolorization is complete the acid is replaced by forty-five per cent alcohol, and the preparation carried through the same series as before to absolute alcohol, cleared in clove oil, and mounted in canada balsam.

It is often convenient to allow a certain number of dissections to accumulate before staining them, as a dozen or so can be carried through with little more trouble than a single one. They keep perfectly well in Bless' fluid. In decolorizing, select the least dense of the batch and allow it to remain on the stage of the microscope—in its solid watch glass—examining it from time to time. The remainder need not be looked at until this is ready. As each specimen is decolorized it should be carried up to seventy per cent alcohol, and allowed to remain there till all are ready, when they can be mounted together. Decolorization may take many hours; it should not be hastened unduly by using a stronger acid, or the sharpness of the stain will be lost.

Instead of haematoxylin, borax carmine stain may be used. It gives excellent results.

Brilliant results can be obtained by this method by noting the avidity with which different tissues take up the stain, and so adjusting the period of application and the decolorization as to bring out the special point desired. For instance, muscle fibre takes up carmine readily, but is easily decolorized, so that if a piece of gut is stained for only a few hours, and then carefully decolorized, the circular and longitudinal fibres are beautifully shown up, the cells remaining unstained. By treating another piece for a longer time, and preferably with haematoxylin, the cells in the wall can be shown without any of the muscles. Similarly with the ovaries, a few experiments will enable one to show up the nurse cells, the apical filament, or the marginal epithelium. All three cannot be shown satisfactorily on the same preparation. Every tissue has its own peculiarities, which must be learned by experience, but successful preparations show so much more than can be learned from fresh tissues, and are so useful in confirming sections, that they are well worth the trouble involved.

If it is not convenient to carry out the whole operation at one time, the preparation may be taken rapidly through the intervening alcohols to seventy per cent, and allowed to remain there till it can be completed. Staining, and sometimes decolorization, may be allowed to go on overnight.

Section cutting

Sections may be cut in either paraffin or celloidin, or by the combined method. The former is applicable to soft tissues isolated from the chitinous parts, and the latter to whole parts of flies. The ordinary celloidin method, though it has its advantages, has the very great disadvantage that serial sections cannot be cut without a great deal of trouble.

In cutting ordinary paraffin sections of isolated portions of tissue, difficulties are chiefly met with on account of the small size of the part and of the close association of the air-containing tracheae with the tissue. The former difficulty is best got over by staining with eosin previous to clearing; a minute drop of watery eosin added to the first change of absolute alcohol will make the part pink enough to be seen when in the clearing agent and in the paraffin block. Tracheae should be dissected off as far as possible before fixation, and the part should always be examined carefully with a lens while in the paraffin bath to ascertain if there are any bubbles of air still adhering to the tracheae. If they are present they can usually be detached with a hot needle.

Paper boxes* are the most satisfactory moulds for the paraffin blocks, as they permit of much more manipulation than anything else. Watch glasses (not the solid kind) are sometimes used, but they are not usually deep enough to get a homogeneous block. They should be smeared with glycerine before use, to prevent the wax adhering to the glass. When the tissue is ready for embedding, the paraffin wax should be heated in a pot to a temperature slightly above the melting point, and poured into the paper box; the tissue is then transferred with a pipette or with forceps, and arranged as desired for section cutting. If the wax begins to set before the correct arrangement is obtained it may be melted again by a wide bore pipette, heated in the flame. As soon as the tissue is in position the paper box should be placed in a large vessel of cool water. Always use an excess of paraffin.

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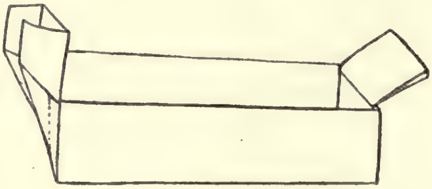
* Paper boxes for embedding, as shown in the text-figure, are made as follows. Take a piece of paper—preferably India paper—about twice as long as broad, and make two folds in the long direction, thus reducing the diameter to one-third; double down each end of the folded paper in two square folds, pressing them flat with the finger nail or a paper knife. Now open out the paper flat. It will be seen that there are six squares at each end, in transverse rows of three, and three oblong areas, which are to form the sides and bottom of the box, in the middle. Bend up the squared ends till they are perpendicular to the bottom, and make a diagonal crease in each of the corner squares, so that the side and end walls of the box come in contact with one another. The squares with diagonal folds now form triangular flaps on the outside of the box, and should be folded back so as to overlap one another, as shown at the left side of the figure. The outer sets of squares, which are now superimposed on one another, form flaps which serve as handles, and also provide a convenient place on which to note the details of the contents of the block. If several specimens are to be embedded in the same block the paper from which the box is to be made should be longer in proportion.

When working in hot climates tissues should not be cut out of the moulds until they are required for section cutting, as the continuous high temperature melts the wax sufficiently to round off the straight edges which are so essential for obtaining good ribbons. The name of the preparation, date, etc., are written on the outside of the paper.



TEXT FIGURE 3.

As in all fine histological work, the more quickly the embedding process is carried out the more satisfactory are the results. The periods used in ordinary pathological work are far too long for small pieces of delicate insect tissue. Everything depends upon the size and density of the tissues, and no rules can be laid down ; the periods which have been found satisfactory for the mid-gut of the mosquito may be taken as an example :—Fixation in Bless' fluid, five minutes ; seventy per cent alcohol, five minutes, with two changes, to wash out the acid ; eighty per cent, ninety per cent, and absolute alcohol, five minutes each, with two changes of the last, the first containing a minute trace of watery eosin solution ; xylol, three minutes, or till cleared ; paraffin, of as low a melting point as the climate permits, five minutes.

Use of the copper plate

In view of the short period of immersion and the small size of most entomological specimens the paraffin bath is not so convenient to use as the copper plate method devised by Stephens and Christophers. All that is required is a slab of copper three inches broad and about a foot long, mounted on a tripod and heated at one end by a spirit lamp. A series of watch glasses—preferably solid ones—is placed on this, each containing paraffin wax, and a point is found on the slab at which the wax is melted and no more, the next watch glass containing solid wax. The specimens are dropped into the wax with a pipette, and are readily accessible.

Double embedding

The double embedding process should always be used when dealing with a part which contains chitin, such as the proboscis, or when cutting sections of the thorax to show the presence of filariae. It is the only method by which serial sections of whole flies can be cut. The principle of the method is to impregnate the parts with a solution of celloidin, and then to embed in paraffin. The celloidin supports the tissues and holds them together, while the paraffin enables serial sections to be cut in the ordinary way. The preparation is brought into absolute alcohol after fixation, and then placed for eight to twelve hours in a mixture of equal parts of alcohol and ether. It is then transferred to a one per cent solution of celloidin in alcohol and ether for twenty-four hours, and to a three per cent solution for the same period. It is an advantage to replace the thin celloidin with the thick very gradually, adding a little now and then, till finally the whole is changed into a fresh three per cent solution. In cases where serious difficulty in cutting sections is met with, it may be necessary to pass from one-half per cent celloidin to four per cent over a period of four days. When impregnated with the celloidin the tissue has to be placed in cedar oil, and in order to avoid exposure to the air while this is being done it is best to pour the oil into the tube with the celloidin, decanting it carefully down the side. In a day or less, the tissue, which at first lies at the junction of the two fluids, will sink into the oil. It should be left for some hours after this, to ensure thorough clearing. It is then embedded in paraffin in the ordinary way, and for as short a time as possible, as both the chitin and the celloidin, get very hard if heated much.

It is often extremely difficult to get a good series of sections of chitinous parts, and many trials have to be made before the correct method is hit upon. If the preparation is kept too long in celloidin the soft tissues shrink away from the chitinous framework, which also becomes brittle, while if it is not kept long enough the parts will not remain coherent when the razor passes through them. The amount of time for the paraffin bath is the most difficult factor to determine. If the material is left in it too long the chitin becomes brittle and the finer details of the soft parts are lost through shrinkage, while if the time is too short the paraffin does not penetrate. The margin between the two extremes is very small, and has to be determined by experiment for each particular tissue. For this reason it is advisable to start with as many specimens of the same material as possible, and to give each a different length of time in the bath, noting the time given to the best sections for future experiments. The results are not very satisfactory at the best, and it is seldom that one can obtain a perfect series of sections of a whole insect or tick. For practical purposes all the information required can usually be obtained by sectioning the parts separately.

Advantage should, whenever possible, be taken of the fact that the chitin of a newly emerged insect is soft and cuts well; though reagents will not penetrate it at all readily.

Razors

Perhaps the most important detail in the whole technique of cutting sections is the sharpening of the razor. Even the best razors are of little use as they come from the maker, the edge being much too abrupt and wedge-shaped. They should be ground down on a *soft* stone, lubricated with a plentiful supply of filtered petroleum. It is convenient to fit up a burette over the stone, so adjusted that a constant trickle of oil falls from the tap, the oil being poured through filter paper in a funnel at the open end of the tube. The old edge of the razor comes off in shreds, which must be carefully removed from the stone, or they will spoil the new one. When the razor presents a perfectly smooth and unbroken edge under the microscope, and will cut a hair longitudinally, it should be finished off on a strop, first with razor paste and then without. If one portion of the blade gets chipped in cutting a hard part, the razor can be moved a little to one side in the holder, so that a new portion comes into use; by doing this a single razor can be used through a series without further stropping. It may take a whole day to sharpen a razor properly.

In order to make the sections adhere to the slide a fixative composed of equal parts of glycerine and white of egg is used; a very small quantity of this being smeared over the slide. This makes the slide sticky, and some care is necessary in placing the rows of sections on it, for once they are laid down, it is not easy to rearrange them.

Stretching and mounting sections

For straightening out the sections and making them adhere to the slide the following procedure is at once quick and effective. A small quantity of water, freshly boiled to expel the air, is placed on the slide with a fine bore pipette, and allowed to flow all over till all the sections are wet. The copper plate used for embedding is previously heated up to about the melting point of paraffin at the hottest end. Some odd pieces of section, not required, and not necessarily containing any tissue, are then taken, and placed on a slide with a small drop of water. A large drop of water is then placed on the heated copper, and the trial sections on their slide are lowered on to it. If the copper is too hot, they will melt, and another trial must be made at a point further away from the flame. A place is soon found where the sections at once straighten out to their full extent without melting. The slides full of sections are now placed on this point one by one, care being taken that there is always a film of water between the copper and the glass, and a sufficiency of water on the slide. The sections straighten out in a second or two, and should at once be removed. In doing this always tilt up the end of the slide which is on the copper first, and not the end which is in the fingers, or the sections may flow from the slide to the copper. Remove the superfluous water with a pipette or filter paper, and leave the slides to dry overnight.

In dealing with serial sections a great deal of time and trouble can be saved by mounting a large number of sections on the same slide. The upper and lower edges of the block should be trimmed very carefully in order to get a straight ribbon, and this should be laid out on large sheets of paper till the whole has been cut. A piece of card is then taken and cut to a size two-thirds the length of the coverslips which are to be used for mounting. Using this as a measure, cut up the ribbon into lengths, with due care lest the order in which they lie should be disturbed. The cut should be made with a sharp knife with a thin and perfectly clean blade, otherwise the sections will adhere to it. Now take a camel's hair brush, moisten the tip slightly, and apply it to one end of one of the pieces. It will adhere, and the row of sections may be lifted up and laid on the slide, near one edge. Then take the next row, and lay it parallel with the first, and so on till the slide is filled as full as it will hold, each row of sections touching its neighbour. The first section should be placed at the left hand side of the slide, at the point which will correspond with the left hand top corner of the label; the first section of the second row is next to the first of the first row, and so on. In this way a hundred or more sections can be mounted on a single slide. The particular order does not matter, so long as the worker adopts a uniform one for all his sections.

The examination of insect tissues for parasites, either natural parasites or pathogenic haematozoa, should be carried out in a methodical manner. There is a right and a wrong way of doing it, and as the tissues are delicate and will not stand rough handling, and as the process may have to be carried out many hundreds of times, much trouble will be saved and more reliable results obtained by adopting a regular routine.

The examination of tissues for parasites

Preliminary examination

The method of dissection has already been described, both in the general remarks embodied in this chapter and in the systematic accounts of the various forms, and the technique may be taken up at the point at which the part to be examined has been isolated on the slide. Clear away all that is not required, such as fragments of the exo-skeleton and fat body, and then place a hair beside the dissection ; lower on to it a coverslip, and examine first with a low power. The use of the hair is to prevent the pressure of the coverslip from distorting the tissue, or driving out the contents. It saves trouble to keep a small collection of bristles of different thicknesses, from cattle, buffaloes, or pigs, in a tube for this purpose. When the coverslip has been lowered it will probably be necessary to add more saline, to expel any air bubbles which may have been included. Never attempt to drive them out by pressure, but use excess of saline, subsequently sucking up what is not required with a pipette or filter paper.

With a low power the general appearance of the gut should be noted carefully. With some practice one can learn to distinguish infected gut and Malphigian tubes by their greater opacity, and to pick out the pieces which require further examination with a high power. If necessary the coverslip can be ringed with vaseline for a more prolonged examination. A No. 6 objective, with a high power eyepiece, will generally suffice, but an oil immersion lens can be used, if the precaution is taken to have a thin coverslip. A high power dry objective is most useful. The preparation may be examined at this stage with a dark ground illumination.

Having ascertained the presence of the parasite in a particular piece of tissue, the next step is to isolate that piece for a closer examination, and for staining. Remove the coverslip by flooding the slide with saline and inserting the point of a needle under one corner of it, pipette off the excess of saline, and place the slide under the dissecting microscope. Then with a pair of sharp needles cut out the part required, and remove it to a clean slide, with a small drop of saline. It can either be lifted up with a needle, or with a pipette. A needle is the best, as there is always a risk of the tissue sticking to the glass of the pipette. The needle should be perfectly clean and well smoothed down on a soft stone, or the tissue

Isolation of infected part

may adhere, and perhaps be broken as it is being detached. It is most important to remove the isolated piece, and not to attempt any further manipulations on the slide which contains other tissues. The piece may be further examined at this stage with a high power and without a hair, if required, but in this case it must be remembered that if parasites are seen free from the tissue it may be only because they have been detached by pressure.

Smearing out

To prepare for staining proceed as follows. Using as small a quantity of saline as it is possible to work with without the preparation becoming dry, open the organ with a fine needle, to allow the organisms to escape. If they are extracellular, the gut can then be removed with a needle, and the minute drop containing them held at once over the mouth of the bottle containing the osmic acid fixative. Fixation does not take more than a minute. Then smear out the drop with a piece of coverglass broken to a convenient size, endeavouring to get as small a smear as possible, so as to have the parasites collected in one place. As soon as it is dry place the slide in absolute alcohol for fifteen minutes, after which it is ready for staining.

The making of the smear must be done rapidly in the tropics, to avoid the preparation getting dry before it is fixed. Pieces of broken coverglass should be kept ready for use.

If the whole of the organ is smeared out on the slide on which the dissection was originally carried out the parasites get mixed up with the tissue, and in the case of the gut also with the food, and not only do they stain badly, but they are distributed over such a large area that they may be difficult to find. It saves much time in the end to remove the part required, and there is also this important advantage, that if parasites are found one can be reasonably sure which part of the insect they came from.

If the parasite is intra-cellular, the tissue containing it must be teased out under the dissecting microscope, and then smeared out with a piece of coverslip. Often a hollow organ, such, for instance, as the hind-gut of a fly or a diverticulum of a tick, can be spread out flat and dragged along the slide in just a trace of saline till it is almost flat. If fixed and stained in this position the wall of the organ is thin enough to enable one to see the parasites through it. Endeavour to use the natural juices of the tissue as much as possible, and a minimum of saline.

The examination should be by no means restricted to one part of the insect or tick. Examine all the organs in rotation, at least in the preliminary part of the work, and examine them separately.

It is difficult to make proper smears of a gut which is full of blood, and if circumstances permit it is better to wait until most of the blood is digested. This applies especially to the examination of the gut of *Anopheles* for the parasites of malaria.

Eggs are also rather difficult to examine. The egg may be ruptured with the point of a fine capillary pipette, and the fluid so obtained blown on to a slide, fixing it at once ; or the egg may be smeared out in the ordinary way.

Coverslips are not satisfactory for ordinary use. Even when the utmost care is taken, they get so brittle in the tropics that they become impossible to handle with safety, and they have no advantage over slides sufficient to compensate for this.

Much has been written about the necessity for keeping the film wet throughout all the fixing and staining process. The results obtained by different observers are very discordant, and there is good reason to doubt many of the statements made on the subject. Fixation with osmic acid and absolute alcohol, drying, and the use of Romanowski's stain, are sufficient as a routine practice. Special methods may be used to meet particular circumstances, and for these the numerous papers on the subject should be consulted.

The osmic acid fixative is conveniently kept in a bottle the mouth of which is just a little narrower than a slide. The upper surface of the mouth should be ground down on a smooth stone, so that when the slide is in position over the bottle the vapour will not escape.

In the tropics the greatest care is necessary to keep absolute alcohol anhydrous. Anhydrous copper sulphate, prepared by heating ordinary blue stone till all the water of crystallization is driven off, should be kept in the bottle, and replaced by fresh salt as soon as it acquires a green tint.

CHAPTER XII

THE RELATION OF ARTHROPODA TO THEIR PARASITES

THE fundamental conception underlying the relations between blood-sucking arthropods and disease is now so well known that there is no need to explain it in detail or to quote instances, many of which are familiar to every medical man. Briefly, it rests upon the existence of a number of protozoa, pathogenic to vertebrates in many instances, the life cycle of which is made up of two phases, one of which is passed in the tissues of the vertebrate and the other in the tissues of an invertebrate. The linking up of the two phases of the cycle is brought about, in the great majority of cases, by the act of feeding, the puncture through which blood is obtained serving as the point of communication between the tissues of the two hosts.

Dissemination of bacterial diseases, such as cholera, enteric fever, dysentery, and plague, does not come within these limits, since there is no suggestion that a sojourn in the body of an insect is of advantage to the organisms. The rôle of the insect in these cases is to a large extent a mechanical one, infection being brought about by mere surface contact; it may be partly due to the faculty which these bacteria possess for existing, though probably not for multiplying to any great extent, in the alimentary tract of the carrier. The transmission of plague by the flea, for instance, is not due to any fundamental change undergone by the bacillus in the alimentary tract, but to its capacity of multiplying and retaining its virulence until it is passed out with the faeces at the time of feeding, and therefore in the neighbourhood of an abrasion of the skin. These cases have been discussed in their respective chapters as far as they fall within the scope of the present work, and need not be referred to again. The question of mechanical or 'accidental' transmission of protozoal parasites will be dealt with later.

It follows from the nature of the case that the study of these diseases is inseparably bound up with the study of the insect host of the causal organism, and the great increase of interest in entomology which has taken place within recent years bears witness to the recognition of this connection. A full knowledge of the bionomics, life history and breeding habits of the invertebrate carrier is essential for a proper understanding of the epidemiology of the disease, and forms the foundation for all rational preventive measures. It is not, perhaps, quite so clearly recognized that an equally intimate knowledge on the same subjects, and in addition a close acquaintance with the anatomy of the invertebrate, often down to the minutest details of cell structure, is required for the study of the parasite itself, during that stage of its existence in which the body of the invertebrate constitutes its environment. A study of the morphology of the parasite alone, though it may bring to light, facts of great scientific interest, cannot be expected to lead to a complete knowledge of its life history and conditions of existence, since these are inevitably dependent on the life history, habits, and bionomics of its hosts.

Importance of normal histology

The study of the internal structure of the invertebrate host is of particular importance, as it furnishes a valuable control for experimental observations, and enables one to avoid some at least of the many pitfalls which beset the path of the worker in this field. Unfortunately it is in this direction that the greatest difficulty is met with. The subject has received little attention within recent years, and for much of the information at our disposal we are indebted to a past generation of scientists, who carried out their observations, often with very imperfect apparatus but with an accuracy which is astonishing, at a time when parasitology in its modern sense did not exist. Much more work in this direction is urgently needed, and until it has been done some doubt must always attach to observations on the more minute stages of protozoa parasitic in insect tissues. The disputed points regarding the life history of spirochaetes will occur to the reader in this connection : the phenomenon of 'granule shedding' in vertebrate blood is not excessively difficult to follow, because the observer is familiar with the normal appearance and constituents of the medium in which the organisms lie, but phenomena of a similar nature taking place in insect tissues demand the greatest reserve in interpretation. It cannot be claimed that our knowledge of the normal histology and physiology of these tissues is more than the merest fragment of the truth ; the study of them has lagged far behind that of the protozoa which infect them.

When dealing with the blood-sucking arthropods it has to be remembered that they are exceptional members of their group, and cannot be expected to conform to the usual type. The habit of feeding on blood is associated with many other features both of structure and life history which are common to many forms from widely separated families, and connected, sometimes very obscurely, with the parasitic habit. Reproduction, for instance, often takes place in a very aberrant manner, as in the pupiparous flies and in the still more remarkable instance of the bed bug. Generalizations from the study of allied but non-parasitic forms have to be made with great caution.

Relations between parasite and its two hosts specific

The relations between the protozoon and its two hosts are to a certain extent specific, that is to say, a given species of parasite has for its alternate hosts two particular species or their near allies. The parasite of malaria, for instance, occurs only in the blood of man and is transmitted only by certain species of mosquito of the genus *Anopheles*; the parasite of Yellow Fever is transmitted only by *Stegomyia fasciata*, and there is no reason to believe that it occurs in any animal other than man. There is seldom, however, a hard and fast line, either as regards the vertebrate or the invertebrate host; *Filaria bancrofti*, for instance, can develop in several species of different though allied genera of Culicidae; according to Brumpt human trypanosomiasis (*T. cruzi*) in Brazil can be conveyed by the bed bug as well as by *Conorhinus megistus*, which was at first believed to be its only host; several species of *Phlebotomus* appear to be efficient in the transmission of Phlebotomus fever; *Trypanosoma gambiense*, usually transmitted by *Glossina palpalis*, can also be transmitted by *Glossina morsitans* (Taute), while *Trypanosoma brucei*, the usual host of which is *morsitans*, can develop in *palpalis*. An equal latitude is to be observed in the relations between the parasite and its vertebrate host; *Trypanosoma gambiense*, for example, is found in the blood of a considerable number of mammals in the region in which the disease is endemic; *Piroplasma gibsoni*, normally a parasite of the jackal, also occurs in the dog; most laboratory animals can be infected with various species of trypanosomes and spirochaetes.

Reservoirs of Infection

The occurrence of a given species of protozoal parasite in a number of different vertebrates introduces a question of considerable importance, as each of these constitutes a source from which individuals of another species may become infected. It will be observed that when a given species exists in several species of hosts, its effect may vary with the kind of host in which it is living. In the instances quoted above, the trypanosome which causes fatal sleeping sickness in man is without effect on many species of antelope, while *Piroplasma gibsoni*, which is fatal to most dogs, and particularly fatal to fox-hounds, is harmless to the jackal, in which it normally occurs. From the point of view of the parasite it is a question of adaptation, and the ideal host would be one in which no effects likely to shorten the life of the host, and thereby diminish the chances of passage to the invertebrate, are produced. Pathogenicity, in fact, is a sign of imperfect adaptation, and if a fatal disease were always produced, the continuance of the race of the parasite would be endangered. Vertebrates in which no disease is produced, such as the antelope and the jackal in the instances given above, are to be regarded as the true hosts of the parasites, rather than man and the dog.

The importance of this from the entomological point of view lies in the fact that blood-sucking arthropods are not restricted to one species of animal for food, but will feed on many different and often widely separated species. It is not, therefore, sufficient to determine which species of invertebrate can act as a host; it is of almost equal importance to ascertain on what vertebrates other than the one in which a disease is produced the transmitter will feed in a state of nature, and what are the conditions which influence it in its choice of food. Information on these points is surprisingly scanty even with reference to the commoner blood-sucking insects.

It should be noted that the protozoa which produce such serious effects on their vertebrate hosts appear to be quite harmless to the invertebrate, and do not shorten its life; the tolerance appears to be mutual, for the infection is not thrown off once it has become established, and may continue to the end of the life of the insect, a constant supply of the infective stages being kept up by multiplication and development. One transmitter may therefore be capable of infecting a large number of vertebrates.

THE HABITAT AND MOVEMENTS OF PARASITES WITHIN THE INVERTEBRATE HOST

In both vertebrate and invertebrate host the cycle of development which the parasite passes through is directed, not only to establish it in its new host, but also to provide forms which are able to pass to the alternate host, and there to start the other phase of its life cycle. The alternation of hosts is evidently the means adopted to secure the continuance of the race of the parasite on the death of the infected individual.

One of the essential differences between true transmission of parasites and mere mechanical infection is that in the former case a definite interval elapses between the ingestion of the infecting meal and the time at which the transmitter becomes capable of infecting a vertebrate host. During this interval or latent period, which may be only a few days, as in the case of Malaria and Yellow Fever, or may extend to many weeks as in Sleeping Sickness, the parasite is undergoing a cycle of changes which result in the production of the infective form. While it would be out of place to discuss these changes here, it will be of considerable interest to consider the sites at which they may take place, and the means which the parasite may eventually adopt to leave the body and to enter a fresh vertebrate. But before going on to this subject the case of 'accidental' or 'mechanical' transmission must be referred to.

'Mechanical' or 'Accidental' Transmission

This term is applied to those cases in which there is neither any specific relation between the parasite and its insect host nor any multiplication or cycle of development undergone during the passage from one vertebrate to the next. It is in fact mechanical infection by the proboscis, or perhaps by the legs or body, such as might be produced experimentally in the laboratory, the organisms adhering to the proboscis and passing to the next animal on which the insect feeds. Several trypanosome diseases, among which may be mentioned 'debab', a disease of camels in the Soudan, in which various species of Tabanidae are suspected as transmitting agents by the Sergents, are believed to be spread in this way. The haematophagous Muscids, on account of their habit of feeding on the juices which exude from sores on the host, and on the blood exuding from the punctures made by other flies, may also act as mechanical carriers of infection, as appears to have been the case in the epidemic of 'murrina' recorded by Darling from the Panama Canal Zone. The possibilities of this kind of transmission are necessarily limited. Most biting flies take a full meal at each feed, and seldom feed more than once a day, so that the parasite cannot be passed on to a second host unless it is capable of living during this period in what would appear, judging from the behaviour of such organisms under laboratory conditions, to be a very unfavourable environment; or if it happened that the fly was interrupted in its meal, and settled on another individual to complete it. The intermittent habit of feeding of the non-biting muscids suggests that they are more likely to spread infection in this way than are true biting flies. (See page 348.)

The precise locality selected for the site of the cycle of development varies with the different classes of parasitic protozoa, and it will serve our purpose best to take a general case, and to follow the movements of an organism from the time it is ingested with the food to the time at which it passes back to the vertebrate, noting in passing, the cases in which theoretical possibilities fall into line with experimental observations.

Habitat of Parasite

The stage of the parasite which is infective for the invertebrate always passes into the alimentary tract with the food, but there are several routes by which the stage infective for the vertebrate may reach its destination, and it will be convenient to summarize these at the start. The following possibilities present themselves:—

Passage of Parasite from Invertebrate Host to Vertebrate

1. The parasite may leave by the route at which it entered, that is, the food canal in the proboscis.
2. It may leave by the salivary duct in the proboscis, which, it should be noted, is *entirely* shut off from the food canal.
3. It may leave by the anus, being passed out with the excreta.
4. It may leave by the genital aperture; only the case of the female need be considered here. In this event it passes to the next generation, and must still leave by one of the other routes to reach the vertebrate.
5. It may leave by rupture of the body wall. This may take place at any part, or at a particular part, and may result in the entry of the parasite at an abrasion of the skin, or into the alimentary tract of the vertebrate when the latter swallows the invertebrate host.

It will be evident that, with one point of entry and several of exit, the possibilities as regards the situation of a parasite within the body of its insect host are considerable. The simplest case is that in which the whole cycle is passed in the lumen of the gut. According to Bouffard and Roubaud, *Trypanosoma cazalboui* never passes beyond the proboscis of the tsetse fly which transmits it, the whole cycle being carried out in the space between the labrum-epipharynx and the hypopharynx, which in these flies is constantly filled with a liquid believed to be salivary secretion. The infective stages pass into the new host at the time of feeding. In other cases the organisms pass into the mid-gut and hind-gut, and may leave the body either by the proboscis or the anus. According to Roubaud, *Trypanosoma dimorphon* and *pecaudi*, after a period of development in the hind-gut, pass again forwards towards the proboscis, through which they leave the body for the vertebrate host. Robertson has recently shown that the same cycle is observed in the case of *Trypanosoma nanum* and *T. pecorumn* in *G. palpalis.*

Parasites in the Faeces

Exit of the parasite per anum is probably a commoner and is certainly a more easily understood event. Infection in this case is dependent on the well known habit of defaecation at the time of feeding, or immediately after it, which is to be observed in the great majority of blood-sucking insects. The mechanism of the alimentary canal is apparently a very simple one, the mere entry of food into the anterior parts being sufficient to set up a peristalsis along the whole length of the gut, with the result that the contents of the more posterior parts are passed out on to the skin of the host while the meal is still in progress. In many cases, and especially among the Diptera, a drop of red and apparently unaltered blood is passed out towards the end of the meal. The excrement thus voided is of course in close approximation to the wound made by the mouth parts, and may mingle with the drop of blood which oozes out when the proboscis is withdrawn, so that there is ample opportunity for the parasite, especially if it is motile, to pass into the tissues of the invertebrate through the wound. This is, in all probability, the means by which the spirochaete of relapsing fever passes from *Ornithodorus moubata* to the vertebrate host, as has been shown by the experiments of Leishman and Hindle, though in this case it should be noted that the infective fluid is probably the secretion from the Malpighian tubes. Exit per anum is also the common event in the natural flagellates of insects, which are either voided on the food of the adult and thereafter taken up by another individual, or pass out in such situations that they may be taken up by the larva with its food.

Many parasites do not remain free in the lumen of the gut. They may, as in the case of *Trypanosoma lewisi* described by Minchin, become intracellular at one stage of the developmental cycle, and again become free. In other cases, of which the parasite of malaria offers a good example, they pass into the wall of the gut and remain there for a time. The spirochaete of African Relapsing fever, according to Leishman, undergoes a part of its development in the cells of the Malpighian tubes of the tick, eventually leaving through the anus as indicated above.

Passage of Parasite to Haematocoele

In the more complex cases the parasite leaves the gut altogether by penetrating the wall, and passes into the haematocoele. Subsequent events depend on conditions of which we have little knowledge, and this stage of the development is usually the one which has been the least clearly defined. It is clear, however, that one of three things must happen; the parasite (1) may remain in the cavity, (2) pass back to the gut at a later stage, or (3) pass to some other organ. The first is apparently what happens in the case of *Spirochaeta obermeiri*, which, according to Nicolle, Blaizot and Conseil, is not found in the alimentary tract of the louse after the lapse of a few days after the infecting feed, and is not found in the salivary glands or ovaries at any time. The only exit from the body in such a case is by rupture of the body wall, and according to the above observers this is what actually occurs ; the louse is crushed by the person who harbours it, and the liberated spirochaete finds its way into the blood through an abrasion. It is possible that some protozoa, especially such as have for their hosts the more sedentary parasites, may find their way into the tissues of the vertebrate by a similar route ; the presence of the invertebrate host irritates the vertebrate, which endeavours to free itself, and in doing so either swallows the invertebrate or ruptures its integument with its teeth, thus enabling the protozoon to enter either the buccal or the gastric mucous membrane. According to Strickland, rats may become infected with *Trypanosoma lewisi* by swallowing its invertebrate host, the rat flea. The case of *Filaria bancrofti*, and probably of many other filariae, is rather different. Here the infective stage is free in the haematocoele, but passes forwards to the proboscis, and is set free at the seat of the wound, in some manner which has not yet been determined.

Should the parasite not remain free in the haematocoele, it must pass to one or other of the organs. How readily this may occur will be understood at once by recalling the nature of the haematocoele and of the circulation. The haematocoele is little more than a potential space, all the organs of the abdomen being tightly packed together exactly as in the case of more complex animals ; the Malpighian tubes, which are diverticula of the gut, are usually very long, and are twined in and out throughout the cavity ; the same is often the case with the salivary glands, which, as in *Glossina*, may be almost entirely abdominal. A glance at the sections figured on Plate XXV will show at once how intimate are the relations of the abdominal organs to one another, and how easily a parasite which retained its motility after passing through the wall of the gut might penetrate any one of them. Further, the blood in this space is kept in a state of constant movement by the action of the heart, which drives it forward through the aorta and draws it back again through the pericardial space, so that no matter at what point the organisms penetrate the wall of the gut they will, unless they penetrate other organs and so anchor themselves at once, be distributed all over the cavity.

The only organs in which parasites have actually been found are the salivary glands and ovaries: whether they actively seek out or are attracted to these particular organs, or whether they penetrate all indiscriminately but can only survive in these, is a question which does not appear to have attracted attention.

Parasites in the Salivary Glands

The passage of a parasite from the gut to the salivary gland has not been actually demonstrated, but it may be safely assumed that it takes place by way of the haematocoele; indeed, no other route is conceivable in view of the anatomy of the parts. The length of time the parasite remains free in the haematocoele, and the form which it assumes while free, are questions to be decided in each case. In the case of the parasites of malaria it is always assumed that the sporozoits are liberated into the haematocoele of the host, a species of *Anopheles*, and find their way into the salivary glands, penetrating through the basement membrane, on the rupture of the oocyst; the exact route by which they reach their destination is obscure. Presumably parasites reach the ovaries by a similar route in the case of hereditary transmission.

Another route from the gut to the salivary glands has recently been suggested by Miss Robertson in the case of *Trypanosoma gambiense* in *Glossina palpalis*. This observer states that, after a preliminary multiplication and differentiation in the gut, the trypanosomes pass forward to the proventriculus; there is some difficulty in reaching this situation, however, and they only remain there so long as the fly is not subjected to too long a fast. From the proventriculus they pass to the hypopharynx, and up the duct to the glands. It is stated that the 'penetration of the trypanosomes into the salivary glands occurs quite clearly 'from the hypopharynx, and the successive stages of the process can be 'seen very well in the live state, in careful dissections at the appropriate 'period'; and further, that 'slender trypanosomes may in rare cases be 'seen lying in small numbers, free in the hypopharynx of flies whose 'salivary glands are not yet infected. They then come back along the 'narrow duct of the salivary glands, and can be seen there as free-swim'ming slender creatures'.

With the protozoological aspect of the question we are not at present concerned, but it is necessary to point out the anatomical difficulties which lie in the way of such an explanation. In the first place, the salivary apparatus of *Glossina*, as of *all* Diptera, is entirely separate from the alimentary canal, the only point in common between the two being that they open at the prestomum, that is, at the extreme tip of the proboscis. Although the food channel in the proboscis and the salivary duct in the hypopharynx are in close apposition, they are quite distinct channels, and communication between the two is *only* established at their openings, if at all. It is clearly necessary, therefore, that the trypanosomes, if they do not penetrate the wall of the gut and make their way to the salivary glands from the outside, must pass up the food channel to the tip of the proboscis and then turn round the corner and make their way back in the reverse direction up the hypopharynx. In other words, they pass through the valvular proventriculus, up the empty and contracted oesophagus, through the pharynx and the connected sphincter muscles, which are specially designed to prevent the forward passage of the contents of the gut, and down the narrow channel between the labrum-epipharynx and the hypopharynx; they then turn directly backwards, past the valve formed by the patulous tip of the hypopharynx, up the salivary duct and through the salivary valve, designed to permit of only a forward flow of the saliva, and into the glands. Further, during all this time they must necessarily travel in the reverse direction to the normal flow of the contents; if a feed of blood is taken while they are passing forwards they will have to maintain their position against a relatively enormous mass of blood, quickly absorbed; if they have reached the salivary duct they will have to maintain their position against the flow of saliva.

It should be noted further that the wall of the alimentary tract in the anterior portion would be much more difficult of penetration than in the lower parts. All the fore-gut is lined by a chitinous intima, and the pharynx and the parts in front of it are relatively very stout. If the trypanosomes pierce the wall at all the most probable situation would be in the mesenteron, where there is no chitinous lining and where the wall is being constantly weakened by the denudation of cells in the process of digestion. The failure to find trypanosomes in the body cavity is, of course, no proof that they were absent at all times. It is reasonable to suppose that if only a few reached the glands they might establish a permanent infection.

It is not easy to accept the hypothesis that a parasite can pass forward to the proboscis and so into the blood of a vertebrate host at the time of feeding; it is infinitely more difficult to believe that having reached the proboscis it should again pass backwards, when it might quite well attain its destination by passing directly into the blood.

The presence of the parasites (not necessarily in stages which would be infective for the vertebrate) in the ovaries leads to hereditary transmission, many clear examples of which have been demonstrated.

The parasite remains passive in the egg until it is hatched, and develops at a later stage, so that the second generation becomes infective; infection of the third from the second generation may occur, and so on indefinitely. It is often a matter of considerable difficulty to obtain individuals free from infection for the purposes of experiments. As examples of hereditary infection *Piroplasma canis* and *bigeminum*, and *Spirochaeta duttoni*, all transmitted by ticks as already stated; *Crithidia melophaga*, a natural flagellate of *Melophagus ovinus*; *Crithidia haemaphysalidis* from *Haemaphysalis bispinosa*, may be mentioned.

Hereditary Transmission

Hereditary transmission is not of course final, as the parasite has still to reach its vertebrate host. In the case of those arthropods which are blood-sucking and parasitic in all the instars, as are the ticks, this introduces still further complications; any one or more of the instars may be the stage at which the parasite is taken up from the vertebrate, and any of the succeeding stages of that or the next generation may pass it back again. In *Piroplasma bigeminum* only the adult female *Margaropus annulatus* can serve to take up the parasite, which is returned to a new host by the young larva; the nymphs may ingest the parasite transmitted by the larvae and if dislodged may infect another animal. One may imagine still more complex conditions in connection with those ticks which feed on different species of vertebrates in their several instars.

The occurrence of any one of these methods of transmission does not of course exclude the others, though it is probable that in each case one method is usual, others being adopted more or less by accident. In the early experiments on the transmission of *Trypanosoma gambiense*, for instance, mechanical infection was found to occur, though very irregularly, and was thought to be the usual method. Three methods of transmission of *Trypanosoma lewisi* have been demonstrated, by biting ('accidental' infection), by the deposition of infected faeces on the skin of the rat, and by the eating of the invertebrate host by the rat.

In experimental observations with known transmitters and susceptible animals it is not usual to find that all become infected, even though the experiments are carried out under apparently natural conditions. The reasons for these apparent failures are in many respects obscure. The temperature at which the experiments are carried out has an undoubted influence in most if not all cases, either affecting the length of the latent period, or even totally inhibiting the cycle of development. The parasite

Conditions determining infection

of Kala Azar, for instance, will not continue to develop in the bed bug except within a narrow range of temperature. Kinghorn and Yorke have shown that the development of *T. rhodesiense* in *G. morsitans* is directly dependent on the temperature to which the flies are subjected. The age of the invertebrate also comes into play; in a proportion of the individuals infected under natural conditions the length of life remaining to the host may not be enough to allow of the completion of the cycle and the formation of the infective phases; it is also known that with increase in age many changes take place in the tissues of insects, and these may render them unsuitable for the parasite. Other causes may be looked for in connection with the processes of digestion and the nature of the food subsequent to the infecting meal. It has been shown in an earlier chapter that very extensive changes go on in the mid-gut during the secretion and excretion of the digestive fluid, and during the subsequent regeneration of the epithelium. This may affect the chances of a parasite becoming established in many ways. If it is essential that it should become intracellular at one stage of its cycle, its fate would appear to depend on whether it happens to penetrate a cell which will remain in position after the excretion of its secretion, or one which is destined to be cast off and replaced. If the parasite is to pierce the wall of the gut in order to pass into the haematocoele, its chances may depend on whether it happens to reach a part of the wall which is weakened temporarily by the desquamation of its cells, or a part which is still of considerable thickness. As regards the nature of the food, there is some evidence to show that this affects the development of the parasites very materially. The Sleeping Sickness Commission of the Royal Society found that *Trypanosoma gambiense* was present in the blood of the water buck, but in such very small numbers that it could not be detected by microscopical examination, and gave rise to no symptoms; in infected monkeys, on the other hand, the trypanosomes were numerous, and the disease ran a fatal course. One would expect that a much larger proportion of the tsetse flies which were fed on the monkeys would become infected than of those which were fed on the water buck, but the reverse was found to be actually the case. One inference which may be drawn from this remarkable phenomenon is that the blood of the water buck, within the alimentary tract of the fly, constitutes a more favourable medium for the developmental cycle of the parasite than does the blood of the monkey, and that this factor was sufficiently powerful to overweigh the advantage of the greater initial infection. According to Robertson and other observers, the successful infection of *G. palpalis* with *T. gambiense* depends almost entirely on the presence of adult trypanosomes (short forms) in the blood of the vertebrate; such a hypothesis appears to assume that these forms represent some sexual stage, otherwise it is difficult to explain why they alone can produce infection in the invertebrate. A sexual cycle has never yet been demonstrated. Another instance is to be found in the behaviour of *Herpetomonas culicis*, a natural parasite of *Culex fatigans*. The early stages of this organism are passed in the larva of the mosquito, and the fully formed flagellates are found in the newly hatched imagines of both sexes. In caught specimens from infected localities, however, only the males and a small percentage of females are found to harbour the flagellate, and if bred females known to be infected are given a meal of blood the parasites are found to have totally disappeared; this suggests that vertebrate blood is an absolutely unfavourable medium for this organism. Many interesting problems suggest themselves with regard to the effect on the contained parasites when a blood-sucking invertebrate feeds on a series of different species of hosts.

NATURAL PARASITES

Under the term 'natural parasites' are included those organisms which pass through the whole of their life cycle in the invertebrate, and have no alternation of hosts in the sense of the foregoing pages. Such parasites are of very wide-spread occurrence, and are of the greatest possible importance in the study of the pathogenic and alternating forms, since they constitute the most frequent and serious source of fallacy in experimental observations. Apart from this, a considerable interest attaches to them on account of the close relationship which exists between many of them and the pathogenic forms.

Almost all forms of protozoa, including gregarines, coccidia, rhizopods, microsporidia, spirochaetes and flagellates, may be found in the tissues of insects; of these the flagellates are of perhaps the greatest practical importance, on account of the very close resemblance between them and the stages of trypanosomes of animal origin which are found in the same situations in the insect. Such parasites are found in all classes of Arthropods, blood-sucking and non-blood-sucking; for experimental purposes, in fact, it is a safe rule to assume that all insects have their natural parasites, though all individuals are not affected. Even such exclusively parasitic forms as ticks and lice are infected, though not so commonly as the less specialized groups.

The life history of these parasites—here referring particularly to the flagellates—is generally simple. They are confined to the alimentary tract of the host, and usually to the hind-gut. In due course a stage is reached when the parasite is fitted, by encystment or otherwise, for a more or less brief exposure to the external atmosphere, and it is then passed out with the faeces. This occurs in such a situation that the young form which is to start a fresh infection can reach its host, for, as in the protozoa of a more complex life history, the parasite is dependent for its continued existence on the habits and bionomics of its host. Defaecation may occur at the time of feeding, so that the infective stages fall upon the food and are in a position to be taken up by the next fly which feeds there, as in the well known instance of *Herpetomonas muscae domesticae*; or the parasites may, in the blood-sucking forms, be passed out with the faeces on to the skin of the host of the arthropod. In the latter case their chance of reaching the alimentary tract of another insect is much greater than would at first be thought. It has been pointed out in connection with several groups of Arthropods in previous chapters that particular species exhibit a marked preference for certain parts of the skin of the host; some species of Tabanidae are constantly found feeding on one part, other species on another, and the same is the case with lice and fleas. The localization of the individuals of the host species is all to the advantage of the parasite where infection is dependent on such contamination, as is the almost universal occurrence among blood-sucking arthropods of the habit of defaecating while feeding. *Tabanus striatus* is one of the flies which has been observed to select a particular site on the skin of the host, and its parasite, *Crithidia tabani*, is almost certainly transmitted in this way. A similar means of transference is readily understood with regard to gregarious insects.

The parasite may not be confined to the imaginal stage, but may occur in the larva, and may be transmitted from larva to larva and from larva to adult. This occurs in the case of *Herpetomonas culicis*, already referred to. Here again the parasites are dependent for their propagation on the habits of the host. *Culex fatigans*, like most of the members of its family, rests during the day in dark and preferably damp situations, and the male may often be seen in considerable numbers near secluded collections of water, probably attracted there by the newly hatched females. Their faeces are passed into or near the water in which the eggs are laid, and the contained parasites find their way into the gut of the larvae along with its food. The parasites are still present in the larva when it pupates, and pass to the imago, where they undergo their final cycle, and produce forms which are capable of infecting the larvae of the second generation. *Spirochaeta culicis* and the spores of gregarines may find their way into adult mosquitoes by a similar route. The spirochaetes and flagellates of fleas also pass through the larval stage of the host.

Hereditary infection occurs among natural parasites as in those with alternate hosts. At least three instances are known in blood-sucking arthropods, *Crithidia melophaga* in *Melophagus ovinus*, a pupiparous fly, *Crithidia christophersi* in *Rhipicephalus sanguineus*, and *Crithidia haemaphysalidis* in *Haemaphysalis bispinosa*.

In view of the wide-spread occurrence and practical importance of these natural parasites it will be of interest to consider briefly their origin and their relation to the pathogenic forms which have a second phase of development passed in the vertebrate host. In the earlier chapters special stress has been laid on the comparative anatomy of the mouth parts of the blood-sucking forms, with a view to making it clear that the blood-sucking proboscis is nothing more than an adaptation of the primitive arthropod structures. The remote ancestors of these forms were in fact provided with mouth appendages adapted, as they are in the vast majority of the modern arthropods, for cutting and tearing, and the food absorbed was solid or semi-solid. Now it is known that almost all collections of water, especially if permanent and rich in organic matter, contain large numbers of primitive organisms; what is the case now was presumably the case at the period when a much larger proportion of the surface of the earth was covered by water than is at present, and it follows that the primitive arthropods were necessarily to a large extent aquatic, as so many of them still are in the larval stage. Protozoa of all kinds would be taken up with the food, and in course of time some of these would become adapted to live and multiply within the body of the arthropod. Once this commensal existence were established, the parasite would share in all the influences to which its host was subjected, and its evolution would proceed *pari passu* with that of its host in accordance with changed conditions.

The occurrence of natural parasites, perfectly harmless to their hosts, in a large proportion of the modern insects is therefore neither very remarkable nor difficult to understand. The question of their relationship to the parasites which alternate between two hosts is a more difficult question, and here we are on very debatable ground. Minchin, to whose opinion due weight must be given, is inclined to believe that those haematozoa which have alternate hosts are primarily parasites of the vertebrate, and would even go further, and maintain that the various species of *Crithidia* found in blood-sucking insects are in reality developmental stages of vertebrate trypanosomes. It must be admitted that there is much to be said for the contrary opinion, that parasites found in insects are primarily their parasites, and that the development of a phase passed in the blood or tissues of the vertebrate or even in the juices of a plant (*Herpetomonas davidi*) is a secondary phenomenon. A study of the comparative anatomy shows clearly enough that the forms with sucking mouths are more recent than those with the parts adapted for cutting and tearing, and in particular that the blood-sucking forms in all orders are more recent than those which are vegetable feeders; the contrary would have to be assumed if the parasites which they contain are to be regarded as derived originally from the blood of vertebrates. To take a precise instance, if the flagellate found in *Musca domestica* is to be regarded as descended from a trypanosome, then *Musca domestica*, its host, must be considered as evolved from a blood-sucking fly, an assumption which is directly contrary to the anatomy of the parts. Further, the occurrence of flagellates which are morphologically true *Crithidia* in flies and other insects which are purely either dung or vegetable feeders can no longer be denied. Another argument is to be found in the effects produced in the two hosts. A large number of trypanosomes are pathogenic to their vertebrate hosts, and as Minchin himself points out, the pathogenicity is a 'disharmony', indicating imperfect adaptation; as no such intolerance is to be found in the relations between parasite and insect host it is probable that the association between the two is of much earlier date. The truth may well lie between these two views, neither of which necessarily puts the other out of court. Before this interesting if somewhat academic question can be definitely settled, very much more will have to be found out with regard to the life histories of both the natural and alternating parasites.

Elimination of Natural Parasites in Experiments

The practical importance of these natural parasites lies, as has already been stated, in the possibility that they may be confused with stages of pathogenic organisms. Their frequency is so great that it is a sound rule in practice *never* to assume that a parasite found in an invertebrate is derived from a vertebrate until the natural parasites have been excluded—often a matter of considerable difficulty. The methods to be adopted vary according to circumstances. Caught specimens, about the history of which nothing is known, should never be used for experiments if it can be avoided. The suspected hosts should be bred from the egg under defined and carefully controlled laboratory conditions, and a proportion of the adults used as controls for the experiments. Even this procedure is not always successful, for some of the natural parasites are transmitted hereditarily through an indefinite number of generations. In such a case controls should be sought for from some other locality, as it is often found that the same species may be infected in one locality and not in another. The same circumstance may be taken advantage of when difficulty is experienced in breeding uninfected individuals on account of the infection of the food supply of the larva. It will be needless to add that breeding from captured larvae is no *certain* means of obtaining uninfected specimens, as the larvae may be infected before they are under control, and may pass on the infection to the adults.

A thorough examination is necessary before one can be certain that parasites are absent. Though natural parasites are usually found in the alimentary tract, they may also occur in the Malpighian tubes, as in the case of the flagellate of *Ceratophalus alladinis*. They may also leave the gut altogether, as must be the case in those which are transmitted hereditarily.

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THE END

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